

RESEARCH ARTICLE

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The oculomanual coordination control center takes into account the mechanical properties of the arm

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Abstract When the eyes and arm are involved in a tracking task, the characteristics of each system differ from those observed when they act alone: smooth pursuit (SP) latency decreases from 130 ms in external target tracking tasks to 0 ms in self-moved target tracking tasks. Two models have been proposed to explain this coordination. The common command model suggests that the same command be addressed to the two sensorimotor systems, which are otherwise organized in parallel, while the coordination control model proposes that coordination is due to a mutual exchange of information between the motor systems. In both cases, the interaction should take into account the dynamic differences between the two systems. However, the nature of the adaptation depends on the model. During self-moved target tracking a perturbation was applied to the arm through the use of an electromagnetic brake. A randomized perturbation of the arm increased the arm motor reaction time without affecting SP. In contrast, a constant perturbation produced an adaptation of the coordination control characterized by a decrease in arm latency and an increase in SP latency relative to motor command. This brought the arm-to-SP latency back to 0 ms. These results support the coordination control model.

Key words Ocular tracking · Oculomanual coordination · Electromyography · Internal model · Human

Introduction

When two sensorimotor systems (arm and eyes) are simultaneously involved in a tracking task, the perfor-

mance of each system changes. Particularly when a subject tracks a visual target attached to his self-moved arm, the static (Steinbach 1969; Gauthier et al. 1988) and dynamic (Gauthier et al. 1988; Vercher et al. 1993) properties of the smooth pursuit (SP) system change. More specifically, accuracy increases (Steinbach and Held 1968), maximum velocity increases from 40° to 100°/s (Gauthier et al. 1988) and the latency decreases from 100–120 ms (eye-alone tracking) to zero (Steinbach 1969; Gauthier and Hofferer 1976).

Vercher (1984) and Gauthier et al. (1988) proposed a model introducing a coordination control system (CCS) which uses the arm motor command to synchronize the arm and SP motor systems and the inflow information from arm muscles to increase the SP system accuracy (mutual coupling). Thus the CCS may use two different strategies to coordinate the motor systems: one based on time (phase and lag between target motion and SP) and the other based on gain (Vercher et al. 1993). Recently the CCS model has been implemented, simulated (Lazzari et al. 1997), and tested (Vercher et al. 1997a).

Nevertheless, other models have also been proposed to explain oculomanual coordination. At least two of these models contradict the coordination model to some extent. A first, quite general model (Howard 1971) proposed that synchronization was a consequence of a common command being addressed to both systems. A more specific model known as the common/parallel command model (Bock 1987) added to the scheme of a common command a double organization controlling the interaction: partially in parallel, partially in common. Indeed, since the dynamic characteristics of arm and SP motor systems are quite different, the control systems should be at least partially separate. In Bock's model the common section includes all of the visual signal processing mechanisms. The parallel sections concern only that which is specific to each system. It is important to note that Bock's (1987) model does not allow information from one system to affect the other system directly. The only interaction is through the common part (common command). If the common part

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adapts, this change should affect the two sensorimotor systems in the same way.

Alternatively, the CCS model (Lazzari et al. 1997) proposes a purely parallel scheme, in which the two sensorimotor systems are completely independent. The CCS harmonizes the arm/eye interaction by controlling the signal interchange between the two sensorimotor systems and also by taking into account the dynamic differences between the two sensorimotor systems. This control might depend on learning since as the external conditions change, the internal representation of these mechanical properties must be continuously updated (Flanagan and Wing 1997), and this learning (adaptive) process is certainly based on nonvisual signals such as arm proprioception (Vercher et al. 1996).

Although neither the Bock (1987) nor the Lazzari et al. (1997) model is explicitly provided with adaptive capabilities, the two models (coordination control and common/parallel command) suggest different predictions regarding the way in which the metasytem would react to mechanical perturbations of the arm. In fact, running numerical simulations of the models while changing the external conditions helped us determine what parameters should be changed to maintain the performance. The present study was aimed at testing these predictions, with unexpected or sustained perturbations of arm movement execution. The prediction of each model is outlined below.

If a common command were sent to both arm and eye motor systems, unexpected perturbations of the arm would not be taken into account, and the eyes and arm no longer be synchronized. If the perturbation were applied systematically, however, arm inflow would allow the arm motor system to take into account the perturbation and to adapt. Two possibilities emerge: first, the adaptation takes place within the component specific to the arm (parallel sections) such that no changes would appear at eye level. Alternatively, the adaptation could take place within the common component (common command and/or common representation). For example, the motor command could increase to overcome the perturbation at arm level, and this would result in an earlier movement of both the arm and the eyes because the same adapted command is used to move both. Thus, a decrease in arm motor delay would be accompanied by a parallel decrease in eye motor delay. The result would be that SP would continue to lead the arm as long as the perturbation is maintained.

As in the common command model, the coordination control model predicts that a randomly applied perturbation of the arm motion should not affect SP initiation (SPi) since SP should precede the arm motion. However, if the perturbation were applied systematically, unlike in the previous model, the coordination control model predicts an adaptation of both the arm motor system and the CCS, although possibly in different ways. Because the CCS model considers that the two sensorimotor systems are controlled in parallel but interact with each other, it is possible that different adaptations to arm perturbations take place at different levels (i.e., decreasing the arm

motor delay and increasing the eye motor delay, resulting in the arm-SPi latency being reduced to about 0 ms).

In order to test these predictions, subjects were requested to move their arm and to track a hand-moved target with their eyes. The arm motion was perturbed by means of an electromagnetic brake. The perturbation was applied randomly or systematically. The electromyographic (EMG) signal of one of the arm muscles involved in the movement (biceps brachialis) allowed us approximately to date the arm motor command. Indeed, as EMG activity begins only 24–30 ms after motor cortex activity (Cheney 1985), one may consider that the initiation of the EMG burst is a good indicator of the time of occurrence of the motor command.

Another aim of this study was to determine the way in which the oculomanual system compensates for constantly applied perturbations of arm motion. Based on the CCS model, three hypotheses are proposed and are discussed below. First, the motor command could be temporarily adjusted by the feedback loop bringing the EMG-to-arm latency back to its initial values (without perturbation) while the EMG-to-SPi latency would remain unaffected. The second hypothesis proposes an adaptation at the oculomotor level: the SP latency should increase to equal the EMG-to-arm latency. Finally, a concomitant adaptation of both arm and eye motor commands to the perturbation is proposed by the last hypothesis. All of these hypothetical mechanisms result after adaptation to a SPi-to-arm latency close to nil. Thus it would be difficult to confirm one of the three without a time reference provided here by the EMG signal. [The arm movement is self-initiated by the subject; thus there is no external stimulus or signal to be used as a reference (Vercher et al. 1997b)]. This study is the first experimental demonstration of predictions originating from numerical simulations of the coordination control model proposed by Lazzari et al. (1997). In addition, the analysis of the observed time course of adaptation will help us to provide the CCS model with adaptive capabilities.

Methods

Subjects

Six right-handed subjects ranging in age from 21 to 32 years (four females and two males), participated in the present study. They were naive with regard to the aim of the study. They were also all exempt of known visual or oculomotor disorders.

Experimental setup

The experimental setup is shown on Fig. 1. A complete description can be found elsewhere (Vercher et al. 1996). Horizontal eye movements were recorded with an infrared corneal reflection device (Iris Skalar: bandwidth DC to 200 Hz, resolution 1.5' arc, linearity $\pm 30^\circ$). Arm position was measured with a potentiometer at elbow level. The EMG activity of the moving arm biceps was recorded using surface electrodes (Meditrace, Graphic Controls) placed on the m. biceps brachialis. The EMG signal was preamplified ($\times 10,000$), and prefiltered (high-pass 30 Hz, low-pass 200 Hz).

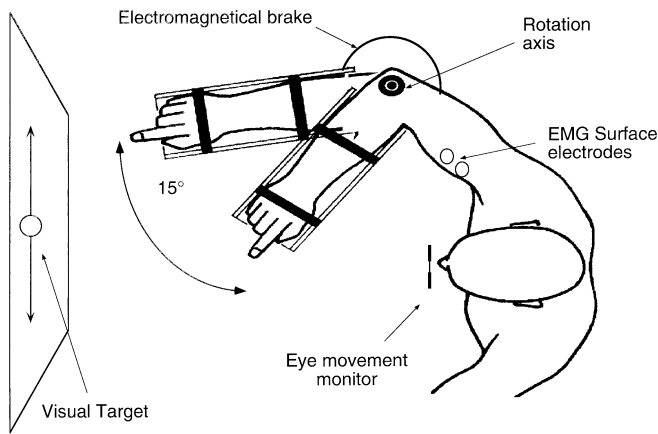


Fig. 1 Experimental set-up

The shoulder was placed in abduction and flexion (about 30°), and the arm/forearm angle was near 100° (Adamovitch et al. 1994) to increase signal/noise ratio. The target, arm, eye, and EMG signals were amplified, filtered (low-pass 250 Hz) and digitized at 500 samples/s. An electromagnetic brake (Warner Electric, model TB 500, maximal torque 40 Nm, tension range 0–20 V) was also positioned on the rotation axis. The brake torque was directly controlled by the computer through a digital-to-analog converter, such that the generated friction was proportional to the tension command. Thus, when the brake was off, the manipulandum needed a torque of 0.44 Nm to be activated. On the other hand, the brake needed 2.66 Nm when 3 V were applied (the relation between the tension and the torque is near to linear in the range 1–17 V). Lacquaniti and Soechting (1986) showed that muscular activation is proportional to the perturbation force.

Tracking task and condition

The subjects were subjected to two conditions during two experimental sessions. The sessions, but not the conditions, were counterbalanced for the subjects. The subjects had to move their right arm back and forth and to track the hand-driven target with their eyes. At the beginning of each trial the subject put the target at the right side of the screen and had to move the arm sinusoidally at about 0.3 Hz in frequency and 15° in amplitude. Subjects were required to maintain target fixation with their eyes. After receiving a “ready” signal from the experimenter the subject started to move the arm. The subject had 3 s in which to make the complete movement. The conditions were:

- Brake off (B-OFF): the brake was fitted to the manipulandum but was not activated.
- Brake on (B-ON): just before the arm movement, a passive friction was applied to the manipulandum. Prior to the session the subjects were instructed to try to maintain the velocity and the amplitude of arm movements in spite of the perturbation. There was no cue to indicate to the subject whether the brake was to be activated or not.

In experiment 1 the two conditions (B-OFF and B-ON) were randomly assigned to the subjects over a total of 120 trials. The brake was always fitted to the manipulandum but activated on an average of only one-third of the trials.

In experiment 2 the perturbation was applied systematically. Subjects completed 100 consecutive trials in three blocks:

- PRE block (preexposure): self-moved target tracking without perturbation (20 consecutive trials in the B-OFF condition)
- PER block (during exposure): self-moved target tracking with perturbation (60 consecutive trials in the B-ON condition)
- POST block (posteffect): self-moved target tracking without perturbation (20 consecutive trials in the B-OFF condition)

The subjects did not know when the change in condition would occur; however, they did know that during the 100 trials a constant perturbation would be applied.

Data analysis

Analysis started with digital low-pass filtering of all signals (cut-off frequency of 30 Hz, -3 dB). The latencies between target and SP motion onsets, EMG burst and arm motion, EMG burst and SP motion, arm and SP motions were measured (target-to-SP, EMG-to-arm, EMG-to-SP, and arm-to-SP latencies). For determination of the SP and arm movement onsets, we used a velocity-acceleration criterion previously described (Vercher et al. 1996). For determination of the EMG burst beginning, we used a similar technique, proposed by Hodges and Bui (1996), after rectifying and integrating the EMG signal. Maximal velocities of arm motion and SP were also determined. In order to test the effect of condition, analysis of variance ($S_6 < c_3 >$) and a Student-Newman-Keuls post hoc test were applied to the data. Since we were interested in SPi, only the trials where eye motion began with SP were analyzed. The others (e.g., starting with a saccade) were rejected. These latter trials represented less than 5% of the total.

Results

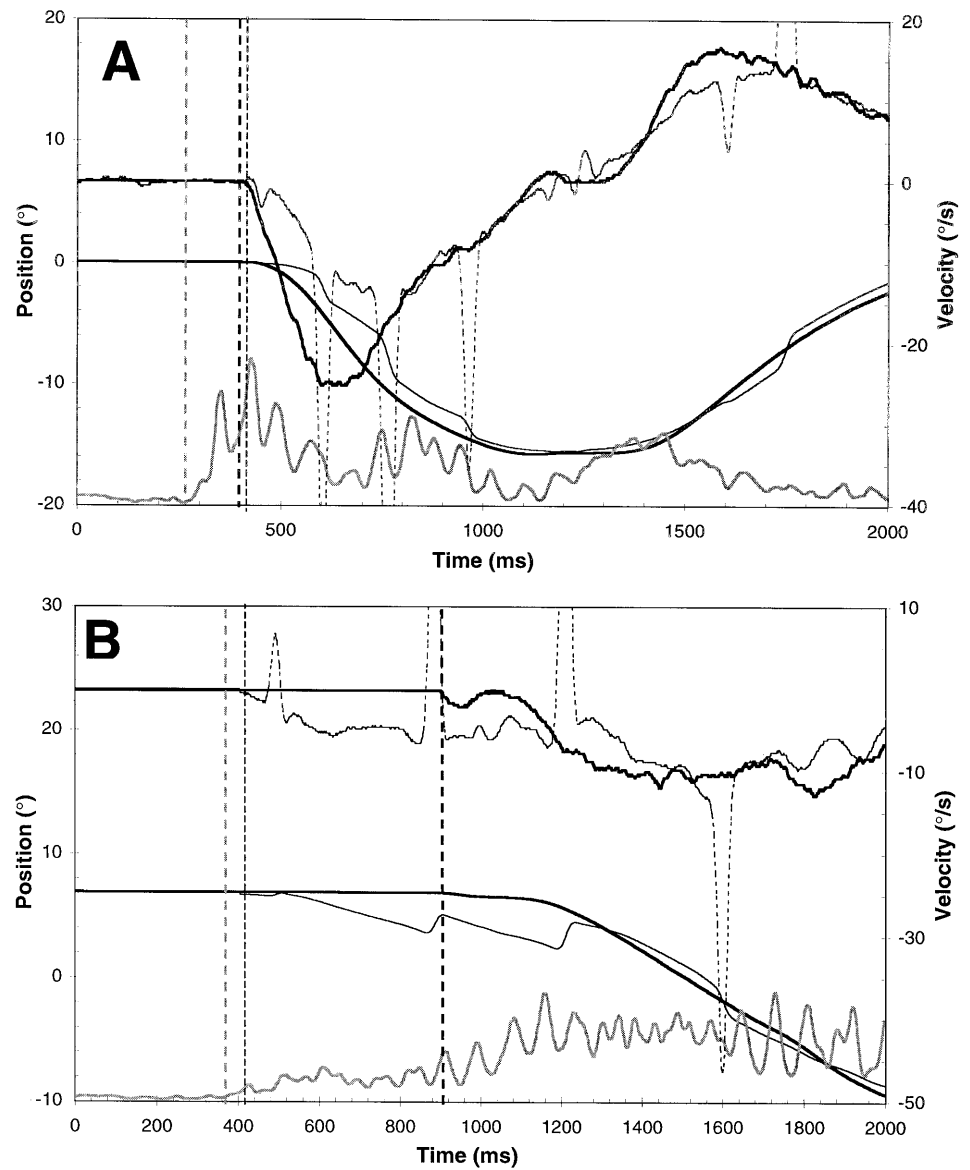
In order to obtain reference data, all the subjects were tested in eye-alone tracking (EAT) and self-moved tracking (SMT) conditions with the brake device being removed (when the brake is fitted but not activated there is still a residual friction). In EAT the target followed an horizontal sinusoidal path (15° , 0.3 Hz). The latencies recorded in the EAT and SMT conditions were not significantly different from previous experiments, i.e., 135 ± 27.86 ms in EAT and considerably shorter, -0.83 ± 25 ms, in SMT (Gauthier and Hofferer 1976; Gauthier and Mussa-Ivaldi 1988; Steinbach 1969; Vercher et al. 1993, 1996).

Experiment 1: nonsystematic perturbation

The aim of the first experiment was to determine the effect of a mechanical arm perturbation on the arm-to-SP temporal coordination. In the B-ON condition (Fig. 2B), SP begins with a latency relative to the arm muscle EMG burst which is similar to that observed in B-OFF condition (Fig. 2A). However, the beginning of the arm movement is delayed relative to the two other events (up to 510 ms after SPi and 650 ms after the beginning of the EMG burst). The delayed arm movement initiation results in an ocular anticipation leading to an increased number of saccades in the direction of the visual target (Fig. 2B).

The frequency histograms in B-OFF and in B-ON conditions (Fig. 3) confirm the delayed initiation of arm motion (relative to EMG and SP motion), showing an increase in arm-to-SP and EMG-to-arm latencies (average and variance). Only the EMG-to-SP latency remains unaffected. Table 1 provides the average latencies for all the subjects and all the conditions.

Fig. 2 Selected examples of oculomanual tracking in the brake off (B-OFF) condition (A) and in the brake on (B-ON) condition (B). Continuous lines, eye (thin) and arm positions (bold); dashed lines, eye (thin) and arm (bold) velocities. Gray bold line at bottom, rectified and integrated EMG of the biceps muscle. Vertical scales correspond to the position (left axis) and velocity (right axis) signals, respectively. There is no scale for the EMG signal amplitude, which values are in mV. Vertical lines, the beginning of arm and SP movements and EMG activity



The analysis of variance showed a significant effect of condition, explaining 68% of the EMG-to-arm latency variance ($F_{1,586}=1255.25$, $P<0.001$), and 72% of the arm-to-SP latency variance ($F_{1,586}=1502.2$, $P<0.001$). No effect was found for EMG-to-SP latency.

A linear regression performed between EMG-to-arm and arm-to-SP latencies (Fig. 4) showed a strong correlation between these two variables ($r^2=0.88$) for the B-ON trials ($r^2=0.91$), not for the B-OFF trials ($r^2=0.01$). A correlation has also been found between EMG-to-SP and EMG-to-arm latencies ($r^2=0.54$) in B-OFF only ($r^2=0.03$ in B-ON).

Thus, these results show that an unexpected perturbation of the mechanical conditions of arm movement execution changed the temporal correlations of oculomanual tracking, particularly the EMG-to-arm and arm-to-SP latencies, confirming that it is indeed the actual arm movement which is affected by the brake, and not the command nor the control.

Experiment 2: systematic perturbation and adaptation

The first experiment showed an effective perturbation of the coordination but did not allow us to distinguish between the coordination models presented in the “Introduction.” The aim of the second experiment was to determine the way in which the oculomanual system behaves when it is submitted to a constant perturbation of the mechanical conditions of arm movement execution. The CCS model predicts that when the system is exposed to a constant perturbation, the system should adapt so as to bring the arm-to-SP latency back to about 0 ms.

Figure 5 shows examples of behavior during the adaptation series. No trial in PRE condition is shown since the same characteristics were found as in the first experiment. The first trial in PER was always similar to trials in B-ON of the first experiment (Fig. 2B). Nevertheless, after performing two-thirds of the trials in PER (Fig. 5A)

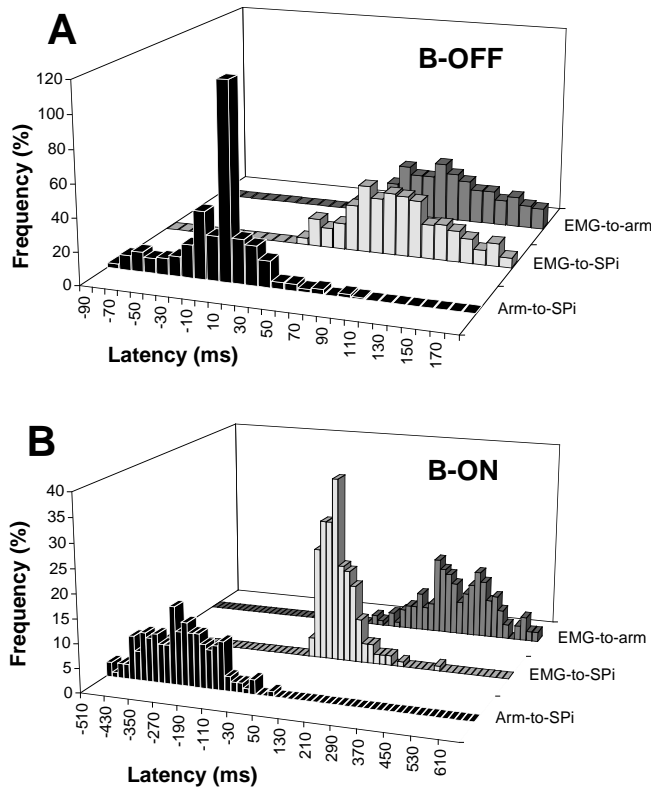


Fig. 3 Frequency histograms of latencies for the trials in the B-OFF (A) and B-ON (B) conditions (all subjects)

Table 1 Tracking latencies in the two conditions (random perturbation): mean \pm SD over all the subjects

Condition	EMG-to-SP	EMG-to-arm	Arm-to-SP
B-OFF	96.4 \pm 47.3 ms	111.1 \pm 50.8 ms	-14.7 \pm 35.7 ms
B-ON	88.4 \pm 48.7 ms	362.1 \pm 120.6 ms*	-273.6 \pm 122.6* ms

* $P < 0.05$

the subjects were fully adapted since their performance at this stage of the adaptation session could not be distinguished from their performance during the B-OFF trials of the first experiment. As opposed to the previous trials, the first trial after brake deactivation (Fig. 5B) always showed a slightly delayed initiation of the SP relative to the arm motion for all subjects. This behavior lasted throughout the subsequent trials in the POST block. However, the number of trials in this block was too small to observe a return to initial (PRE) latencies. Table 2 provides the average latencies, over all subjects and trials in a block.

During continuous exposure to the brake (PER block, condition B-ON), a correlation was found between EMG-to-arm and arm-to-SP latencies ($r^2=0.63$). A correlation was also found (although moderate, $r^2=0.3$) when the brake was turn off (condition B-OFF in POST block), while no such correlation was found in this condition during experiment 1. On the other hand, no relationship ap-

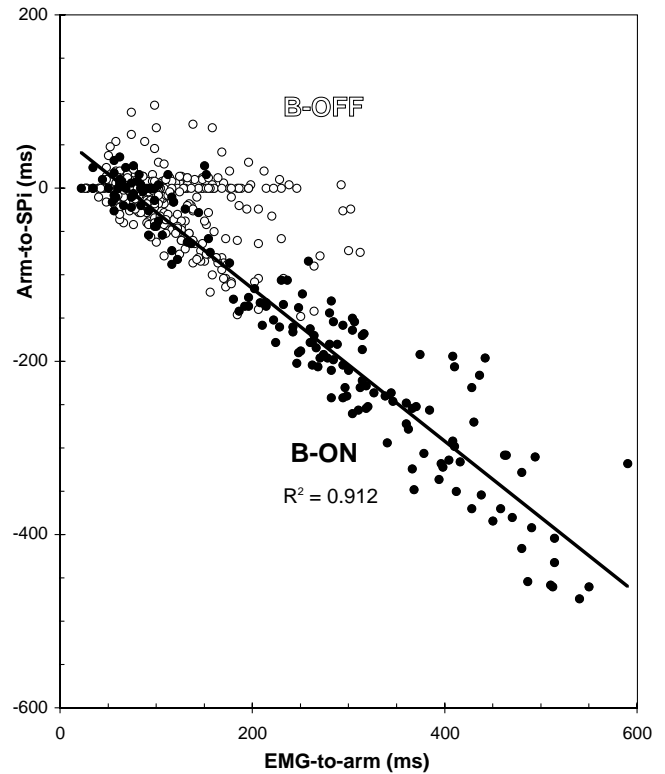
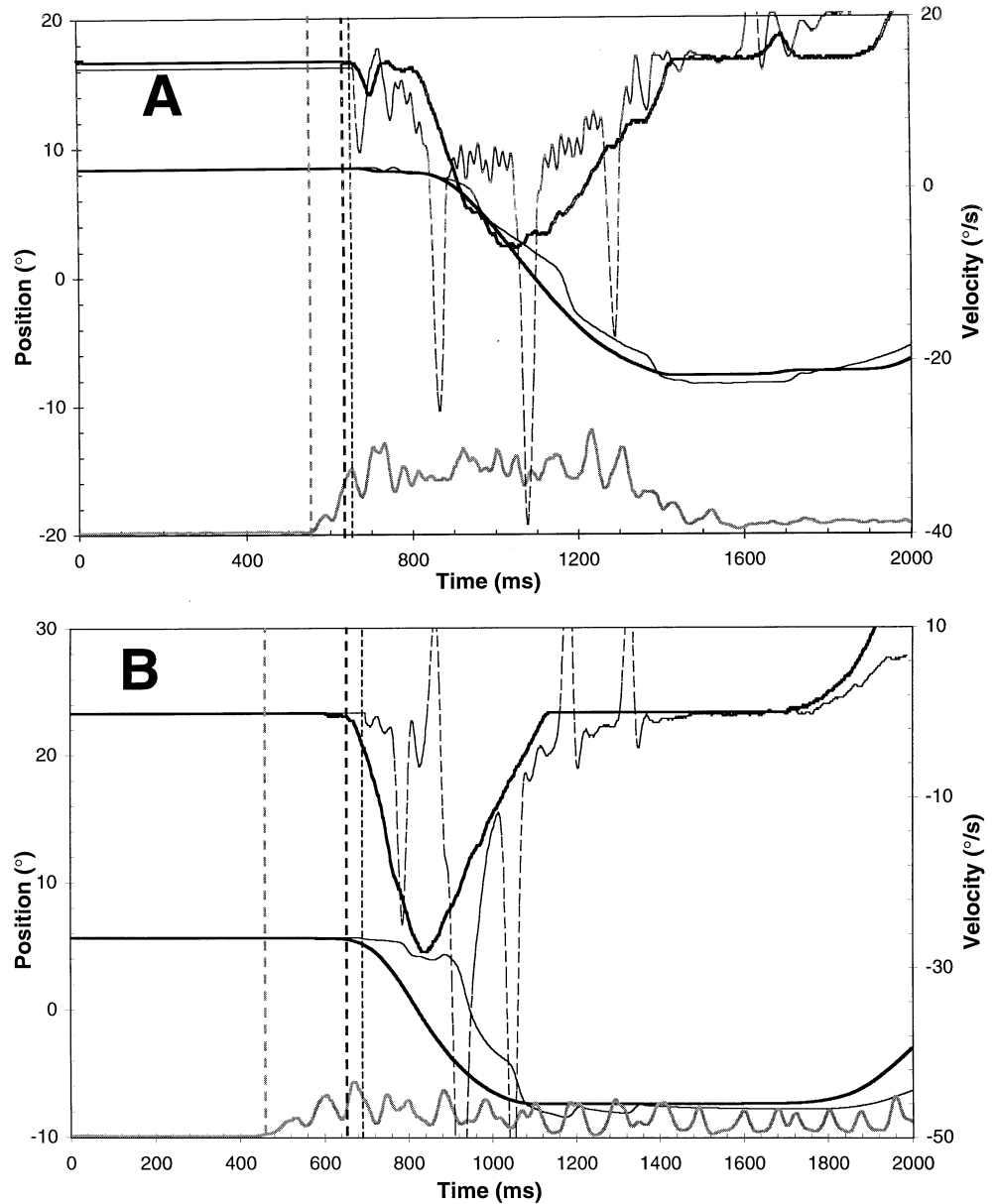


Fig. 4 Correlations and linear regressions between EMG-to-arm and arm-to-SPi latencies in the B-OFF (white dots) and B-ON (black dots) conditions

peared in any of the conditions between the EMG-to-arm and the EMG-to-SP latencies ($r^2=0.16$) nor between the EMG-to-SP and the arm-to-SP latencies ($r^2=0.006$). Analysis of variance showed an effect of condition on EMG-to-SP ($F_{2,584}=12.27$, $P < 0.01$), EMG-to-arm ($F_{2,584}=18.21$, $P < 0.01$), and arm-to-SP ($F_{2,584}=10.40$, $P < 0.01$) latencies. Post-hoc analysis revealed a significant difference between PRE and POST conditions for EMG-to-SP ($P < 0.05$) and arm-to-SP ($P < 0.05$) latencies but not for EMG-to-arm latency. Figure 6 shows the evolution of latencies between the arm and SP motions and the EMG burst in the different stages of the experiment. The figure shows a clear increase in EMG-to-arm latency and a decrease in arm-to-SP latency at the first trial when the brake was unexpectedly on, followed by a progressive return of both EMG-to-arm and arm-to-SP latency to 0 ms during the adaptation session.

Figure 7 shows the time course of arm peak velocity (reached on average 350 ms after motion onset) over trials. The figure shows that the subjects were able to maintain a stable movement pattern except when the brake was suddenly and unexpectedly deactivated. Although the velocity remains constant along the trials (for the three consecutive conditions), it increases by more than 100% in the first trial following the deactivation of the brake. Remember that the subjects were instructed always to produce the same type of arm movement in terms of amplitude, velocity profile and duration. In-

Fig. 5A, B Selected examples of tracking during adaptation. **A** The 40th trial of the adaptation session. **B** The first trial following the deactivation of the brake. Conventions are the same as in Fig. 2



deed, in this experiment we noted a durable and moderate increase in EMG-to-SP latency between the PRE and POST blocks, and a progressive decrease in EMG-to-arm latency during the PER block, both leading to a decrease in arm-to-SP latency between the beginning and the end of the experiment.

Discussion

The coordination control system modeled by Lazzari et al. (1997) and Vercher et al. (1997a) assumes that arm-SP coordination results from a system that is independent of the different sensorimotor systems involved in coordinated tasks. Indeed, one of the most astonishing features of arm-SP coordination is the almost perfect synchrony observed between the eyes and the arm during

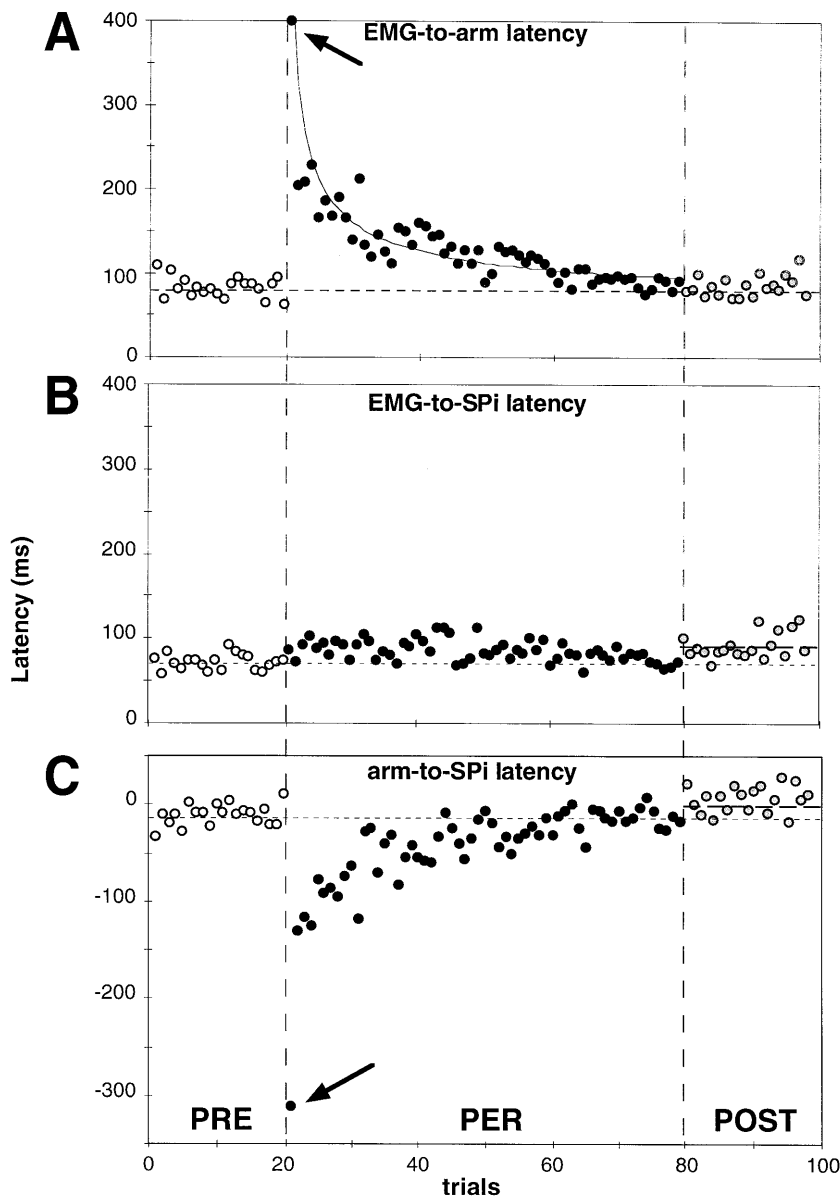
Table 2 Tracking latencies in the three condition blocks (*PRE* B-OFF, *PER* B-ON, systematic perturbation, *POST* B-OFF): mean \pm SD over all the subjects

Condition	EMG-to-SP	EMG-to-arm	Arm-to-SP
PRE	66.3 \pm 23.07 ms	78.80 \pm 30.81 ms	-12.51 \pm 26.10 ms
PER	82.96 \pm 35.83 ms*	108 \pm 61.67 ms*	-25.04 \pm 60.19 ms*
POST	83.31 \pm 36 ms*	84.11 \pm 40.38 ms	-0.80 \pm 33.92 ms*

* $P < 0.05$

SMT tracking tasks in spite of large differences known to exist between these sensorimotor systems. This short latency SP was first observed by Steinbach (1969), who attributed it to previous knowledge of arm motion. Following our theory, intersystem coordination is based on an exchange of sensory and motor signals. Indeed Gau-

Fig. 6A–C Time-course of the latencies (EMG-to-arm, EMG-to-SPi, arm-to-SPi) averaged over all subjects as a function of trial number. *Vertical dashed lines*, transition from one block to the other; *horizontal dotted lines*, the average of the latencies in the PRE block; *horizontal dashed lines* (in the POST block), the average latencies in the POST condition; *arrows*, first trial of the adaptation block



thier and Hofferer (1976) showed that nonvisual signals can trigger and maintain SP of an imaginary target either actively or passively moved by the observer's hand. Gauthier et al. (1988) and Vercher and Gauthier (1988) supported the idea that arm motor signals are used to synchronize the onset of arm motion and SP eye motion.

In contrast, proprioceptive signals appear to play a role in the cross-calibration of eye and hand motor systems once the movement has started (Vercher et al. 1996, 1997b). This was highlighted by a modification of SP system characteristics (maximum velocity, gain, and accuracy) when proprioception is altered (Gauthier et al. 1976, 1988; Vercher et al. 1996). Vercher et al. (1997b) recently proposed that this synchrony could be the result of the CCS taking into account, through arm proprioception, the dynamic differences between the sensorimotor systems, in order to harmonize the temporal relationship during the oculomanual tracking. Note that CCS is not

directly involved in arm control but receives information from both the arm and eye sensorimotor systems. That means that both systems (the CCS and the arm motor system) could adapt independently to arm perturbation but not necessarily in the same way.

SP and arm tracking do not have the same motor delay

Obviously the arm motor system and the oculomotor system differ at both the biomechanical and neural levels. As a consequence, motor delays [defined by Schmidt (1988) as the time between the onset of EMG activity and the onset of a measurable movement] are expected to be longer in the arm motor system than in the oculomotor system. Steinbach (1969) and Gauthier and Hofferer (1976) used this argument to explain the observation that SP leads the hand in self-moved target tracking.

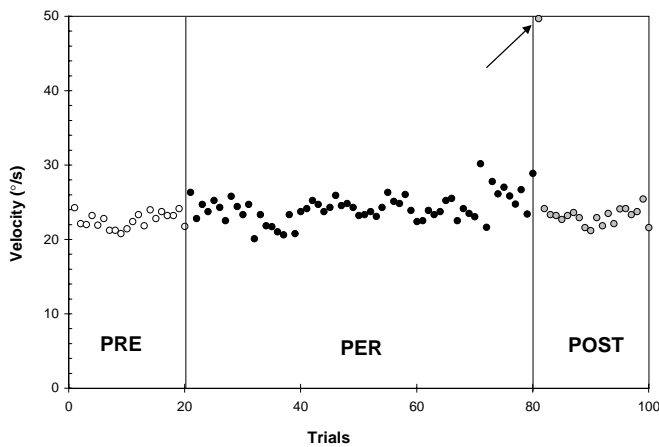


Fig. 7 Time course of arm velocity as a function of trial number averaged for all subjects

They pointed out that if a motor command is sent simultaneously to the eye and finger muscles, the eyes lead the finger by at least 65 ms, due to different conduction and mechanical activation times. However, the SP latency in response to the motion of a hand-attached target is usually much closer to zero than would be expected. It can be proposed that subjects use inflow to be informed of and compensate for the longer motor delay of the arm. A similar interpretation has been proposed by Bard et al. (1992) to explain a difference between deafferented and control subjects in the way in which simultaneous finger and heel movements are synchronized. In response to an external signal both control and deafferented subjects showed a precedence of finger movement over heel movement. In contrast, in a self-paced condition, controls showed a precedence of heel over finger, whereas the responses of the deafferented subject remained unchanged. The authors suggested that control subjects synchronized the inflow signals from the heel and the finger consequent to movement while the deafferented subject synchronized the motor command send to both segments.

Which model best explains SP-arm synchronization?

In the “Introduction” we presented the common/parallel command model as an alternative to the CCS model. Can such a model which is based on the same command being addressed to different systems really apply to eye-arm coordination and even be generalized? Simultaneous eye and head (gaze) movements are certainly controlled by a common, centrally generated command signal (Galiana and Guitton 1992; Crawford and Guitton 1997).

Flanagan and Wing (1997) recently proposed an alternative scheme for intersensory coordination. They showed that controlling the grip of an object and moving (pushing or pulling) it are two functions that share a common internal model of arm/object dynamics. When the manipulandum was made compliant, perfectly synchronous changes in hand trajectory and in grip forces

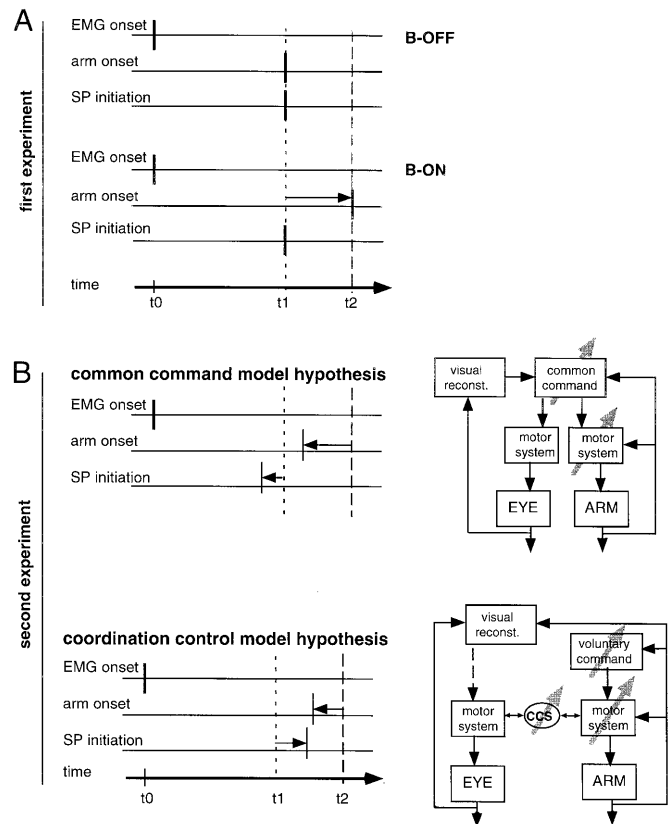


Fig. 8 Schematic representation of EMG-arm-SPi timing as observed with unexpected perturbation (A) and as predicted by the two models in the adaptation experiment (B). To estimate the delays between EMG, arm and SP, the time origin is synchronized with the EMG onset. t_1 is the arm and SP onset in normal condition; t_2 shows the arm onset with unexpected perturbation. The hypotheses are based on the models represented beside the graphs. *Gray arrows in the models*, the element adaptively affected by the perturbations

clearly showed, in the coordinated task used by the authors, that the system controlling grip force makes use of an internal representation of the mechanical properties of the arm/object. A copy of the arm (move) command is addressed to this internal representation in order to estimate (predict) the effect of this command at the mechanical level and to adjust by anticipation the command at hand (grip) level. Moreover, while Flanagan and Wing (1997) did not specifically assess the time course of adaptation over practice, their data showed that this shared internal representation is updated in order to maintain the grip-move coordination.

Several experimental results support the idea that the common command model does not apply to arm-SP coordination in tracking tasks. Indeed, respective latencies of fast eye and arm movements in response to target motion onset are not correlated (Gielen et al. 1984). Gain and phase responses of the arm and the eyes show uncorrelated features (Bock 1987), suggesting the existence of specific commands for each system. Vercher and Gauthier (1988) and Brown et al. (1993) showed, respectively, in monkeys and humans, that lesions of the cerebellum disrupt the coordination between arm and eyes in tracking

tasks while maintaining the ability to produce SP and arm tracking movements in isolation. Van Donkelaar and Lee (1994) showed that SP performance is even worse when cerebellar patients are asked to track a target with their eyes and arm simultaneously.

In the present study the use of a brake at arm level allowed us to further investigate this question by changing the timing between the arm motor command and the subsequent arm motion. Figure 8A is a schematic representation of subjects' behavior in terms of latency during the first experiment. Indeed, when the brake was activated (B-ON condition), the force required to produce an arm movement was increased, thus at least during the first experiment due to the static component of friction, the initiation time of arm movement was delayed. Due to this increased motor delay (from t_1 to t_2), when the perturbation was randomly applied to the arm, the SP eye motion (whose latency relative to arm EMG remained unchanged regardless of the perturbation applied to the arm) largely anticipated the arm movement. This confirmed that SP triggering is under the tight control of the arm motor command. Moreover, the increased variability of arm-to-SP latency was clearly due to the increased variability of arm motor delay, as shown by the correlation between EMG-to-arm and arm-to-SP latencies (B-ON condition). Note that the three latencies are not independent; one is the difference of the other. Thus, if a variable remains constant (here the EMG-to-SP latency), the change in arm-to-SP latency is explained only by the variability of EMG-to-arm latency.

One possible interpretation of the short SP latency in the B-OFF condition is that because the subject himself decided when to move his arm, he knew when the target would move, and he would therefore be able to anticipate target motion. Anticipatory eye movements due to expectation appear when the subject receives a cue to target onset (Kowler et al. 1984), or when the target is presented intermittently (Barnes and Asselman 1992; Kao and Morrow 1994; Barnes et al. 1997). We do not believe that expectation can explain eye-arm synchrony in self-moved target tracking tasks, because in these conditions SP can start as long as 300 ms before target motion (in B-OFF condition) and even 600 ms before in the B-ON condition. Moreover, Barnes and Asselman (1992) showed that anticipatory eye movements need at least three or four cycles of intermittent target presentation for anticipatory eye movements to appear (the SP latency to the first target flash was 95 ms, the eyes lagging the target), whereas an almost perfect synchronicity between the eyes and the arm appears immediately when the target is hand-moved. The same explanation can be proposed for the B-ON condition.

How does the arm motor system take into account the perturbation?

Let us consider now the results from the second experiment (adaptation). As illustrated in Fig. 8B, the main dif-

ference between the arm motor system and the oculomotor system is that the eyes, unlike the arm, are little affected by external mechanical influences (gravity, imposed forces, etc.). The arm motor system is able to react to unexpected perturbations on line (i.e., during the execution of movement; Prablanc and Martin 1992) through feedback mechanisms, while the existence of a similar process at the oculomotor level is still debated (O'Keefe and Berkley 1991; Knox and Donaldson 1993). In the long term, (i.e., during sustained perturbations) both systems show adaptive properties. While on line control is based on the comparison of the command with an afferent signal specifying how the motion is actually executed, the adaptive control usually needs two sources of inflow information, one interoceptive, i.e., proprioception, and one exteroceptive, i.e., vision (Welch 1974; Gauthier 1979). The two compensative mechanisms have been highlighted in this study. During the B-ON trials the subjects were instructed to maintain their arm movement whatever the perturbations. Thus, when the brake was activated, the subjects, because of this instruction, had to increase the force applied to the manipulandum and thus to change the command, until the arm overcame the opposing force (Ghez and Gordon 1987; Cordo 1990).

This dual compensation mechanism is indicated by the gradual 75% decrease in the EMG-to-arm latency during exposure to the brake (PER block). The first trial in the B-ON condition showed a large average increase in arm movement latency (400 ± 200 ms). At the next trial the latency was already reduced by 50% (Fig. 6A). This behavior during the two first trials suggests an on-line control, compensating for the unexpected perturbation. Once the "surprise effect" is overcome, i.e., during the subsequent 58 trials, latency decreased progressively to near control values. Although no "surprise effect" appeared in terms of latency at the offset of the brake, it did appear in terms of arm velocity (Fig. 7). Thus during the first trial of the POST block the feedforward part of the arm command was still set for a perturbed condition. As soon as the movement was initiated, the feedback loop allowed the command to be reset to the unperturbed state. To this concern, the performance during the POST block cannot be really seen as reflecting a posteffect since the arm motor system is not in open loop from a proprioceptive point of view. Only the first trial at brake offset may give an indication of the adapted state. Thus the central nervous system constantly modulates the activation pattern of muscles in order to take into account the external forces (Virji-Babul et al. 1994). However, the lack of a durable posteffect may also be due to the relatively low number (60) of trials, which does not allow a durable adaptation of the motor command.

How does the oculomanual coordination take into account the arm perturbation?

Although data showed that EMG-to-SPi latency significantly increased from the PRE to the POST block, we

did not see a clear evolution during the PER block as opposed to the EMG-to-arm latency (see Fig. 6B). This could indicate that different types of adaptation occur, for example, a progressive process at arm motor level (see previous section) and a more discrete process at eye or coordinative level. The lower part of Fig. 8 helps us to link our results to the hypotheses proposed in the “Introduction,” which were based on the common/parallel command and coordination control models. Again, neither the common command nor CCS models are explicitly provided with adaptive capabilities. At this stage we can only speculate what the effect of adapting a given parameter would be on the overall performance. There is no way to predict from simulations of the model how the adapted state would be reached. A common command model predicts that if the arm motor command is adapted to an imposed impedance, the increased command sent to the arm motor system (which results in a decrease in arm latency: following the force increase, the threshold required to activate the manipulandum is reached earlier) would lead to a similar reduction in motor delay at the oculomotor level (thus decreasing the SP latency).

On the contrary, the CCS model predicts that an adaptation of arm motor system (decreased latency) might be accompanied by an increase in ocular latency. Indeed, during the exposure phase the CCS would take into account the changes in the dynamic properties of the arm, thus leading to a strong adaptation of the SP system (see the EMG-to-SP latency in the POST block in Fig. 6. Posteffects are usually seen as the proof of the existence of an adaptive process, since at this moment the perturbation is no longer applied: the adapted state is reached at the end of the PER phase but may be masked by the on line control). Our results are consistent with the CCS model rather than with the common command model. We observed that the EMG-to-SP latency variations cannot be explained by the effect of the arm command adaptation. The on-line adaptation of the arm motor system has no effect on the oculomotor system or on the CCS: the SP latency is not affected by the randomized perturbation. However, it is clear that the maintenance of the perturbation led to an adaptation of the coordination (see Fig. 6, EMG-to-SP and arm-to-SP latencies change between PRE and POST blocks). Thus at least two levels adapted since the two effects are opposite in value (decreasing for the arm, and increasing for the eye, as shown in Fig. 5B). The double adaptive structure shown here leads to a global decrease in arm-to-SP latency.

What is the role played by afferent information (proprioception) in CCS adaptation?

Our results do not allow us to directly address this question. However, we may suppose that inflow information role is essential. Arm proprioception informs the central nervous system about the existence and the nature of a perturbation (friction, viscosity, stiffness, mass). The role

of proprioception in adaptation to perturbation has been studied with deafferented subjects. These studies showed that the afferent information is necessary for the motor command synchronization during pointing movement (Bard et al. 1992). Interestingly, when an artificial delay is introduced between the arm and target movements in an oculomanual tracking task, subjects without proprioception perceived this visual feedback delay as a mechanical arm perturbation (Vercher et al. 1996). In fact, as long as their arm movement was not visually detected, the deafferented subjects increased their motor command and interpreted the need for more force as being due to a mechanical resistance to their arm movement. During the randomized perturbation our subjects had a similar reaction. The constant friction produced a delayed target movement relative to the motor command, and as a consequence the subjects increased their force to maintain their arm movement. The deafferented subjects participating in the study of Vercher et al. (1996) could have interpreted the target visual delay (relative to their arm movements) according to the most natural situation which could be met by a normal subject. Due to the lack of proprioception they could not sense their arm and distinguish between these situations. In deafferented subjects vision partially replaced the missing information source. Vercher et al. (1997b) recently showed that the EMG-to-SP latency is much more variable in a deafferented patient than in controls, indicating a possible role of arm proprioception in calibrating the temporal relationship between arm and eye motor commands.

Conclusion

Transitory and unpredictable perturbations of arm motion showed that the SP system is not affected (in terms of time of initiation) by the delayed onset of arm movement. This confirms that the synchronization between the arm and SP is not based on afferent (visual or kinesthetic) signals. By submitting the subject to a sustained perturbation we have shown that not only the arm motor system responds appropriately to the perturbation (by both an on-line, feedback based control and an adaptive process), but that the oculomotor system is also affected. The middle-term (few minutes) adaptation process evidenced here may also occur over a longer period: during growth, humans must adapt to the motor segments evolution (size, mass, etc.). The different patterns and time courses of adaptation to dynamic alterations of the arm at arm control level (leading to a decrease in arm latency), and at SP control level (leading to an increase in SP latency), provide support to the existence of a purely parallel treatment. The harmonization of these two sensorimotor systems is achieved by the CCS which takes into account the dynamic conditions of arm movement execution by processing arm proprioception. This signal, together with retinal and extraretinal signals, is involved in the updating of an internal model, thereby allowing the differences and possible alterations of one of the two sensorimotor systems to be taken into account.

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