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Corrective loops involved in fast aiming movements: effect of task and environment

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Abstract In daily living, we continuously interact with our environment. This environment is rarely stable and living beings show remarkable adaptive capacities. When we reach for an object, it is necessary to localize the position of this object with respect to our own body before programming an adequate arm movement. If the target remains stable, the programmed movement brings the hand near the target. However, what happens when the target suddenly jumps to another position in space? The aim of this work was to investigate how rapid aiming movements are corrected when the target is displaced close to movement onset. Our results reveal that rapid movements can be modified and that the efficiency of trajectory amendments vary according to task (directional or direction/amplitude pointings) and environment (structured or darkness). We were most interested in the specific role played by peripheral and/or central feedback information (efferent copy) in the control of aiming movements. The results suggest that the two types of loops are complementary in movement regulation. However, their predominance varies according to the nature of the task at hand.

Key words Aiming · Trajectory amendment · Neural loops

Introduction

In 1899, Woodworth proposed a two-phase motor system in which an aimed movement is composed of a programmed phase (the initial pulse) and a sensory-control phase (current control), which brings corrections to the initial trajectory. Through the years there has been an overall acceptance of the existence of a long visual loop allowing trajectory amendments of reaching movements in the nearby environment (e.g. Vince 1948; Beggs and Howarth 1972; Keele and Posner 1968). It has been further proposed that vision can be used to improve spatial accuracy mainly in the last portion of rapid aiming movements (Christina 1970; Carlton 1981; Beaubaton and Hay 1986; Marteniuk et al. 1987; van der Meulen et al. 1990). The poor efficiency of these peripheral feedback loops in bringing early amendments to arm movements was associated with the fact that visual information took time to process (Keele and Posner 1968).

In the absence of vision, peripheral proprioceptive loops seem also to play an important role in the control of visual-manual pointing (Gibbs 1965). Moreover, deafferented patients tend to execute aiming trajectories that are inaccurate, even at the very beginning of the trajectory (Ghez et al. 1990; Gordon et al. 1995), and significantly more variable than those performed by normal subjects (Forget and Lamarre 1987; Blouin et al. 1993b). Proprioceptive information has been given the role of both updating the internal representation of arm dynamics and controlling the spatial-temporal coordination of muscle activation. It has been proposed that proprioceptive information could be processed in as little as 130 ms (Higgins and Angel 1970; Pardew 1976; Marsden et al. 1978; Newell and Houk 1983).

Since both visual and proprioceptive feedback loops need around 150 ms to process incoming information, trajectory amendments that occur within 100 ms of the initiation of an arm movement are usually thought to be of central origin (Jeannerod 1991). When aiming movements are directed towards a visual target that is suddenly displaced, many authors report early corrections significantly modifying the direction of the aim in less than 100 ms. Since all movements are performed without vision of the arm, it is proposed that internal loops, which compare a copy of the efferent motor command with the target's new spatial position, are able to correct the ongoing motor programme (Cooke and Diggles 1984; Pélisson et al. 1986; Gordon and Ghez 1987; van Sonderen et al. 1989; van der Meulen et al. 1990), thus smoothly bringing

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the arm onto a new defined trajectory (van Sonderen and Denier van der Gon 1990). Flash (1990) has hypothesized that in aimed movement when the target changes, “the initial trajectory plan continues unmodified until its intended completion and is vectorially summed with a second time-shifted point-to-point hand trajectory plan for moving between the initial and new target locations”. Ongoing corrections have also been postulated to be possible through a look-ahead unit that estimates the current plant state and modifies hand trajectories when necessary (Hoff and Arbid 1993; Miall et al. 1993).

For a better comprehension of the characteristics of these internal loops, many authors have adopted a double-step paradigm, wherein the prior goal of an aiming movement is changed during or after motor response initiation. Through the years, two major types of double-step paradigms have been used depending on whether the second step was applied at various delays after presentation of the first target (Megaw 1974; Georgopoulos et al. 1981; Lacquaniti et al. 1983; Gielen et al. 1984; Gisbergen et al. 1987; Komilis et al. 1993; van Sonderen et al. 1988) or during the first saccadic response (Prablanc and Jeannerod 1975; Goodale et al. 1986; Pélisson et al. 1986; Prablanc et al. 1986; Alstermark et al. 1990; Blouin et al. 1995a, b).

Within the first paradigm, the amendment of the arm trajectory could depend on the time interval between target jump and initiation of arm movement (i.e. the Determinant Time Interval “D”; Carpenter 1977). Van Sonderen and Denier van der Gon (1990) proposed that a sudden displacement of a target causes the internal representation of the visual target to shift gradually from the first to the second target location. This internal image is used as an input to the motor programme generator. The central nervous system would therefore programme fast arm movements towards the internal representation of the target. For such a task, experimental data have shown that this D interval must be at least 160 ms for a complete correction of the trajectory, at the very onset of the arm movement. For short D intervals (< 80 ms), the arm response was systematically directed towards the first target location. Finally, with intermediate D values (> 120 ms), aimed movements were initiated towards some imaginary target, localized between the first and second target positions (Barrett and Glencross 1988). Independently of the initial direction of the aim, trajectories were sometimes further amended during the movement. Komilis et al. (1993) hypothesized that motor error was dynamically evaluated during the acceleration phase of a movement directed towards a perturbed target, allowing amendments to the trajectory to be performed during the deceleration phase. Generally, the efficiency of such on-line corrections was closely related to the duration of the movement.

In the second double-step paradigm, researchers synchronized the target jump with the peak velocity of the first saccadic response (Pélisson et al. 1986), thus triggering the target jump during the saccadic suppression interval. Under such conditions and for relatively slow movements (> 450 ms and < 750 ms), total corrections of aiming movements occurred (Bridgeman et al. 1979; Pélisson et al. 1986; Prablanc and Martin 1992). However, some discrepancies are present in terms of the measured kinematics. When perturbed stimuli were presented, Paulignan et al. (1990, 1991) detected a systematic change in the peak acceleration magnitude, whereas Prablanc and Martin (1992) did not find any change in amplitude or in vector orientation. Such discrepancies were attributed to significant differences in movement durations and/or speeds. Duration and speed were also used to explain the results presented by Blouin et al. (1995b), which showed no correction of the primary movement of amplitude aiming when perturbed stimuli were presented, whereas complete corrections took place during the stabilization phase (second submovement). Moreover, the analysis of the kinematics (time-to-peaks and peak magnitudes for acceleration and velocity) revealed no alteration in the structure of the primary movement. Blouin conducted his experiment in the dark, which forced subjects to use an egocentric frame of reference. Since it is not yet clear how aiming errors are encoded, differences in visual environmental cues might also have contributed to the observed discrepancies.

Few experimenters have investigated the importance of environmental visual cues for the execution of precise goal-directed movements. Velay and Beaubaton (1986) observed that, in an open-loop condition (no vision of the moving limb), the presence of a structured visual field significantly improved the aiming performance, compared with aiming movements directed towards targets presented in total darkness. Conversely, Blouin et al. (1993a) did not find any significant difference in the accuracy of aiming movements performed in either environment. However, they did observe that the absence of visual cues induced a longer deceleration phase, suggesting that environmental characteristics had an effect on the kinematics, i.e. on the programming of aiming movements. Therefore, it is still a matter of debate whether or not environment plays an important role in the programming and execution of visual-manual aiming. In a neurophysiological study, Dassonville et al. (1995) came to the conclusion that target localization is based on a combination of exocentric and egocentric visual cues. If one or the other is missing, then coding leads to a reduced accuracy of target localization. In 1987, Paillard already stated that the two systems coded spatial information in parallel. With such a hypothesis, the respective contributions of the exo- and egocentric systems would change with the experimental conditions under which subjects performed (Roland 1979; Roland et al. 1980; Bridgeman 1991) and/or the strategy adopted (Bridgeman 1991; Ratcliff 1991).

When asked to perform aiming movements with various constraints, subjects adopt different strategies. Using grasping and pointing tasks in a double-step paradigm, Carnahan et al. (1993) noted very early amendments in grasping movements, whereas trajectories in the pointing task were left uncorrected. These discrepancies were apparently related to the task at hand since instructions and experimental conditions were maintained identical for both tasks. It could, therefore, be that the differential use of feedback information by the sensorimotor system is determined mainly by the nature of the task. Studying the efficiency of visual loops in the amendment of fast aiming movements, Bard et al. (1990) also proposed that the involvement of various control loops could be task-specific. They used (a) a pure directional and (b) an amplitude-direction aiming task and prevented vision of the limb at different moments of the trajectory. In amplitude-direction aiming movements, their results revealed that occluding the terminal phase significantly increased terminal errors. However, the absence of visual control during the acceleration phase did not perturb the performance of the subject. Conversely, in the task where only directional coding was necessary, vision of the initial portion of the trajectory yielded better terminal accuracy than open-loop control. Few authors have really looked into the specific neural modes involved in the control of different types of movements or parameters that are to be coded. For example, Boucher et al. (1992) suggested that the regulation of direction could be more under the control of proprioception, whereas the amplitude of an aiming movement might be more dependent on available visual feedback.

With this in mind, we decided to investigate the role played by environment and task specificity in the programming and accurate performance of fast visual-manual aiming movements.

Methods

Subjects

Four distinct groups of subjects were formed for each experimental condition. In a structured environment (exocentric frame of reference), (a) seven subjects (mean age 28.2 years) performed a pure directional aiming task and (b) five subjects (mean age 23.2 years) were tested in the amplitude-direction task. In complete darkness (egocentric frame of reference), (c) five subjects (mean age 35.6 years) were asked to make pure directional movement aiming and (d) five others, (mean age 32.4 years) amplitude-direction aiming movements.

All subjects (12 women and 10 men) were right handed and had uncorrected normal vision. They were naive as to the aim of the experiment. They all gave their written informed consent according to university-approved protocols.

Apparatus

Subjects sat comfortably on an adjustable seat, with their chest leaning against a vertical restraint. A 1.5-m hand-held pointer was extended from a universal joint attached to the floor and could be moved freely when extending the arm. For all trials, four light-emitting diodes (LED targets) were fixed at eye-level on a panel above the area accessible to the pointer. The targets were located at 0°, 12°, 18° and 24° in the subject's right hemifield and 30 cm away from the starting position (for more details, see Blouin et al. 1995b). The tip of the pointer and the targets were approximately 1 cm apart when they were aligned. During the entire experiment, subjects bit into a previously imprinted mouthpiece. This procedure allows immobilization of the subject's head during the aiming movements.

The displacement of the pointer was obtained instantly with two linear potentiometers fixed on a concrete wall facing the subject. Small-gauge wires were attached to these potentiometers and to the pointer 3 cm below the tip. The signals from the potentiometers were digitized at 500 Hz and Cartesian coordinates of the pointer were obtained using trigonometric transforms with a spatial accuracy of 0.12% of the distance covered for direction. Position, velocity and acceleration time curves were obtained and filtered through optimally regularized Fourier series (Hatze 1981).

Movement onset was detected by contact rupture when the pointer left the starting position. End of movement, when necessary, was defined as the first moment when velocity dropped under 50 mm/s; this criterion frequently used for determining the end of an arm movement that is not decelerated by contacting a target (e.g. Blouin 1995b; van der Meulen et al. 1990). An eye movement monitor system (Eye-Trac, model 210) was used to record movements of the left eye. Attached firmly to the subject's head, the Eye-Trac monitored the precise position of the eye in the horizontal plane during each trial. The eye movement position was digitized at 500 Hz. Velocity profiles were obtained through optimally regularized Fourier series (Hatze 1981). Saccadic eye movement onsets were marked by hand and defined as the first moment when the velocity increased above 10°/s.

Procedure

Subjects went through 30 familiarization and 45 experimental trials. During familiarization, subjects performed 10 aiming movements towards each single-step target (12°, 18° and 24°). While doing the task, they had full view of their arm and could visually adjust the trajectory on each trial. During experimental sessions, a dark panel was installed between visual targets and subject's arm, forcing subjects to perform in an open-loop condition. At the beginning of each trial, subjects gazed at the central target for either 1, 5 or 2 s. Then, the central diode was turned off simultaneously with the lighting of one of the three peripheral targets. Following the illumination of the peripheral target, subjects performed an ocular saccade and an arm movement as quickly as possible.

For single-step trials, the peripheral target was presented for 1 s. When the diode was turned off, the subject was instructed to bring his or her arm back to the initial hand position. For the double-step trials, the 18° target was always the first target lit. When the eye reached one third of its trajectory (i.e. near the peak of saccadic suppression; Bridgeman et al. 1975) the 18° target was turned off simultaneously with the lighting of either the 12° or the 24° diode (corresponding to the 18°–12° and 18°–24° double-step stimuli). Since target displacement occurred during saccadic suppression, it was not consciously detected by the subject.

Perturbations were randomly presented. For each experimental session, five trials were performed for each of the single steps (i.e. 12°,18° and 24°), and 15 trials were presented for each of the two double steps (18°–12° and 18°–24°). Regardless of the target presented, single- or double-step stimulus, subjects were instructed to both foveate the peripheral target and initiate a rapid arm movement as quickly as possible. Subjects had to keep eye and hand stabilized at their final positions until the target was extinguished. Priority was given to aiming accuracy. However, aiming movements were rejected whenever movement time was slower than 350 ms. The effects of two different kinds of environment on aiming accuracy were assessed. In the structured environment (exocentric frame of reference), subjects performed in a semi-lit room. In the egocentric frame of reference, all trials were performed in total darkness.

Two different aiming tasks were used. In the direction-only task, subjects were required to make a fast ballistic movement towards the visual target until full extension of the arm. The aiming error was measured in mid-flight when the pointer passed the target plane localized 30 cm from the starting point. In the amplitude-direction task, subjects were required to decelerate their movement and to stop precisely under the target. Hand directional deviations from target (in degrees) and deviations amplitude (in centimetres) were used as measures of accuracy.

Indexing of arm trajectory corrections during double-step conditions included terminal positional precision, in both direction and

Table 1 Means and standard deviations for experimental measures, for both environments (structured and darkness), according to tasks and targets

	Environment			
	Structured		Dark	
	Amplitude task	Directional task	Amplitude task	Directional task
Eye latency (ms)				
12°	128 (44)	169 (38)	106 (35)	146 (36)
18°	137 (46)	184 (40)	120 (34)	172 (47)
24°	145 (51)	197 (52)	128 (55)	182 (49)
18°–12°	135 (48)	181 (41)	119 (47)	145 (32)
18°–24°	134 (57)	181 (35)	104 (32)	153 (41)
Arm movement latency (ms)				
12°	250 (49)	299 (49)	250 (56)	302 (73)
18°	249 (43)	337 (52)	252 (60)	292 (56)
24°	267 (43)	329 (57)	271 (53)	297 (62)
18°–12°	249 (56)	334 (59)	273 (56)	271 (66)
18°–24°	251 (44)	336 (58)	246 (49)	276 (57)
Arm movement duration (ms)				
12°	305 (53)	220 (19)	285 (51)	190 (18)
18°	301 (43)	213 (25)	291 (50)	186 (13)
24°	296 (53)	214 (24)	284 (43)	188 (26)
18°–12°	314 (63)	222 (24)	287 (55)	196 (29)
18°–24°	313 (51)	216 (28)	287 (44)	183 (16)
Time to peak velocity (ms)				
12°	109 (12)	177 (13)	118 (14)	149 (22)
18°	108 (10)	188 (24)	121 (19)	141 (17)
24°	110 (8)	192 (22)	121 (11)	145 (12)
18°–12°	108 (9)	189 (23)	118 (13)	149 (26)
18°–24°	110 (13)	190 (23)	120 (12)	144 (18)
Amplitude of peak velocity (m/s)				
12°	2.36 (0.21)	2.39 (0.19)	2.57 (0.42)	3.06 (0.28)
18°	2.4 (0.21)	2.49 (0.24)	2.61 (0.36)	3.2 (0.22)
24°	2.43 (0.2)	2.46 (0.19)	2.66 (0.41)	3.08 (0.43)
18°–12°	2.4 (0.22)	2.36 (0.23)	2.73 (0.34)	3.16 (2.06)
18°–24°	2.43 (0.23)	2.45 (0.22)	2.67 (0.34)	3.22 (0.28)

amplitude. The accuracy of the 18°–12° double step was compared with the 12° single-step pointing, whereas the accuracy of movements towards the 24° single-step target was used as a criterion for the 18°–24° double step. Movement time, magnitude and temporal occurrence of peak acceleration, deceleration and velocity were also used to verify whether a spatial correction of the arm movement led to a change in the structure of the unfolding motor programme.

Data analysis

All dependent measures were submitted to 2 (Environment) × 2 (Task) × 5 (Target) Split-Plot analyses of variance (ANOVAs), with repeated measures on the Target factor. A Duncan's multiple test was used when needed.

Results

Eye and arm movement latencies

Table 1 presents a summary of the main results (means and standard deviations). For eye movement latency there was a significant main effect of Task ($F_{4,18} = 11.81$, $P < 0.01$) and Target ($F_{4,72} = 8.66$, $P < 0.01$). No interaction was significant. Post-hoc analyses revealed that saccadic latencies were longer for the direction-only than for the direction-amplitude task (171 ms vs 125 ms; $P < 0.01$). In all four conditions, saccadic latencies increased with target eccentricity ($P < 0.05$). For the double-step stimuli, we also measured the inter-saccadic delay. For this parameter, only the main effect of Task was significant ($F_{4,18} = 5.26$, $P < 0.05$), the time interval being longer for the direction-only task than for the direction-amplitude task (271 vs 210 ms; $P < 0.05$).

For arm movement latency there was a significant main effect of Task ($F_{4,18} = 10.84$, $P < 0.01$), which revealed that arm latency was longer in the direction-only aiming task compared with the direction-amplitude task (307 ms vs 256 ms; $P < 0.01$). Neither Target main effect ($F_{4,72} = 1.6$, $P > 0.05$) nor Environment ($F_{4,18} = 1.2$, $P > 0.05$) was significant.

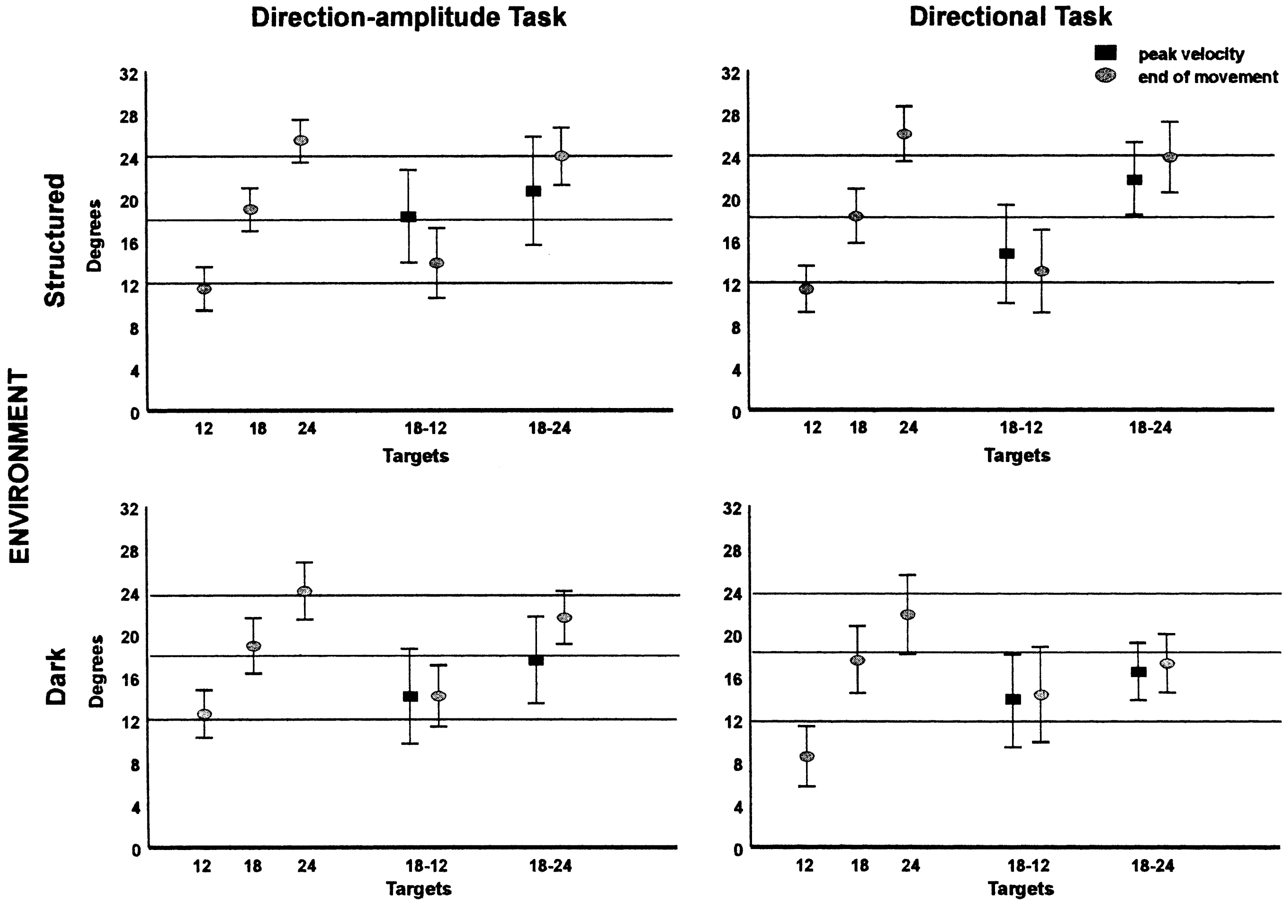

Fig. 1 Means and standard deviations for directional hand position. Each section stands for an experimental condition: direction-amplitude and directional aiming movements in either a structured environment (*above*) or dark environment (*below*). On the X axis are the five targets: 12°, 18°, 24° single-step and 18°–12°, 18°–24° double-step targets. Hand position was measured at two specific moments: peak velocity (*black squares*) and end of movement (*grey circles*). For single steps, movement accuracy was similar at both moments; only terminal hand positions are shown for these targets

Arm movement duration

For arm movement duration there was a main effect of Task ($F_{4,18} = 23.68$, $P < 0.01$), movements being faster in direction-only aiming tasks than in direction-amplitude ones (203 ms vs 296 ms; $P < 0.01$). However, neither the Target factor ($F_{4,18} = 1.50$, $P > 0.05$), nor the Environment factor ($F_{4,18} = 1.76$, $P > 0.05$) was significant.

Hand direction

The focus of the present experiment is to investigate the effect of Environment and Task on the timing and efficiency of on-line amendments brought to fast aiming movements. Double-steps trials did not reveal systematic or abrupt modification of trajectory orientation. Therefore, we decided to calculate aiming precision at specific moments of the movement. Since one of our aims was to see whether the deceleration phase was a component for trajectory amendments, we chose to measure hand direction at the beginning of this phase, i.e. at peak velocity and at the end of the movement. Consequently, directional hand positions were submitted to a 2 (Environment) × 2 (Task) × 5(Target) × 2 (Moment) analysis of variance, with repeated measures on the Target and Moment factors.

Figure 1 illustrates directional hand position at peak velocity and at end of movement according to task constraint in the structured (upper panel) and dark (lower panel) environment. The three-way interaction of the Environment by Target by Moment was significant ($F_{4,72} = 3.93$, $P < 0.01$). The decomposition of the triple (both tasks put together) revealed that in both environments, all single steps were significantly different from each other ($P < 0.01$). For all subjects and all experimental conditions, movements were just as accurate at peak velocity as at the end of movement ($P > 0.05$). Therefore, for single-step movement, the deceleration phase was not used to increase the accuracy of movements. When measuring terminal hand direction, double-step targets were different from the 18° target in all but the 18°–24° target performed in the darkness condition ($P < 0.01$). In both conditions, the 18°–12° targets were significantly different from the 12° target ($P < 0.01$), and the 18°–24° target was also different from the 24° single-step target ($P < 0.01$). This suggests, that, when the target was sud-

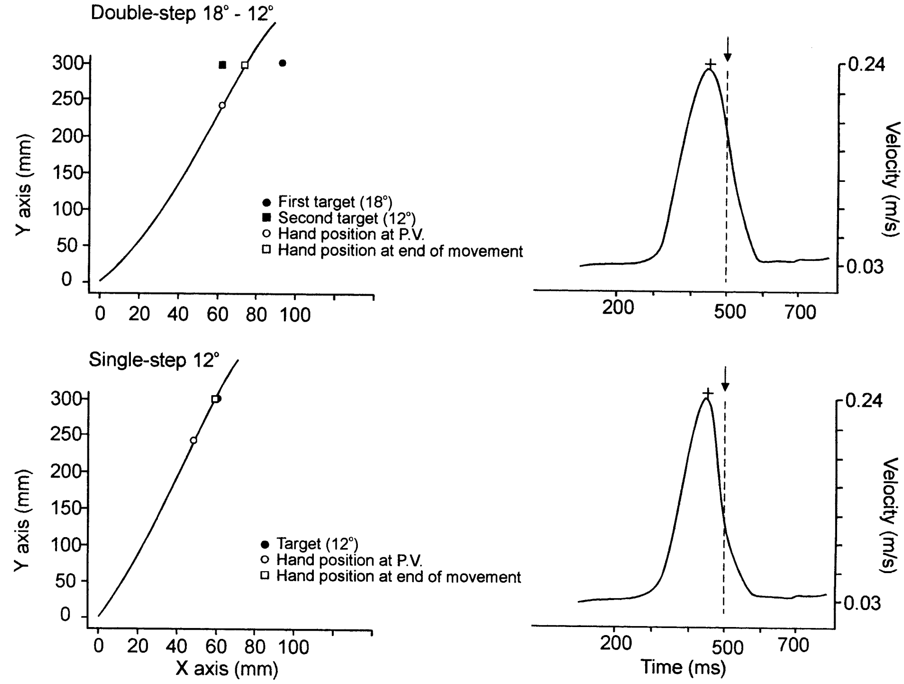

Fig. 2 Typical trajectories and their velocity profiles for movements directed towards double-step and single-step targets while performing a directional task. The *black arrow* indicates when the subject crosses the target plane, marking the recording of the hand position. *P.V.* Peak velocity

denly displaced, subjects were capable of partially correcting their aiming movements.

When measuring hand directions for double-step targets, at both peak velocity and end of movement, we noticed that trajectories towards the 18°–12° double-step target were not corrected during the same movement-phase, when performed in the structured or dark environment. Indeed, in the structured environment, the 18°–12° target was corrected during the deceleration phase (18°–12° and 18° being similar at peak velocity; $P > 0.01$). In darkness, no significant increase in accuracy was measured for the 18°–12° target after peak velocity ($P > 0.05$). However, some corrections had occurred earlier in the movement (i.e. at movement onset or during the acceleration phase), since 18°–12° and 18° targets were different at peak velocity ($P < 0.01$).

The triple interaction of Task by Target by Moment was also significant ($F_{4,72} = 2.85$, $P < 0.05$). Here, we consider hand directional position by averaging results across environments. In the direction-amplitude task, the 18°–12° target was different from both the 18° and the 12° single-step targets at peak velocity ($P < 0.01$). However, at the end of the movement 18°–12° and 12° targets were similar ($P > 0.01$). The 18°–24° target was similar to the 18° target at peak velocity ($P > 0.05$), but similar to the 24° target ($P > 0.05$) and different from the 18° target ($P < 0.01$) at the end of the movement. Therefore, for this task, subjects increased their aiming accuracy during the deceleration phase. In directional movements, even if important aiming errors persisted, no further corrections were brought to the double-step targets during the deceleration phase. Indeed, hand directions were similar, for both double steps, at both peak velocity and end of movement ($P > 0.05$). At peak velocity, the 18°–12° double steps were partially corrected (i.e. different from both the 18° and 12° single steps; $P < 0.01$). The 18°–24° targets were not corrected at all: 18° and 18°–24° targets were similar ($P > 0.05$).

Overall, trajectories were more efficiently amended when visual cues were present in the visual environment than when they were absent. Even when deceleration took place after the subject had crossed the target plan (i.e. in the direction-only task), subjects were able to correct their aiming trajectories. These amendments occurred especially during the first portion of the trajectory (i.e. during the acceleration phase). In the direction-amplitude task, where subjects must stabilize their hand precisely under the target, corrections occurred mainly during the deceleration phase.

Movement kinematics

Since a modification of an unfolding motor programme could be reflected by a modification of its structure, different kinematics parameters were analysed. In the directional aiming task, time to peak deceleration generally occurred after the end of the trial (i.e. after the hand had crossed the target plane; Fig. 2). Consequently, peak amplitudes and time to peaks were measured for velocity only.

Target, Environment and Task factors did not have any effect on the amplitude of the considered peaks ($P > 0.05$). Moreover, main effect of Target was not significant, for time to peak velocity ($F_{4,72} = 0.56$, $P > 0.05$). This suggests that trajectories were not corrected by modifying either the amplitude or the timing of peak. However, the interaction of Environment by Task ($F_{4,18} = 8.64$, $P < 0.01$;) was significant. In directional aiming tasks, subjects reached their peak velocity significantly later than in the

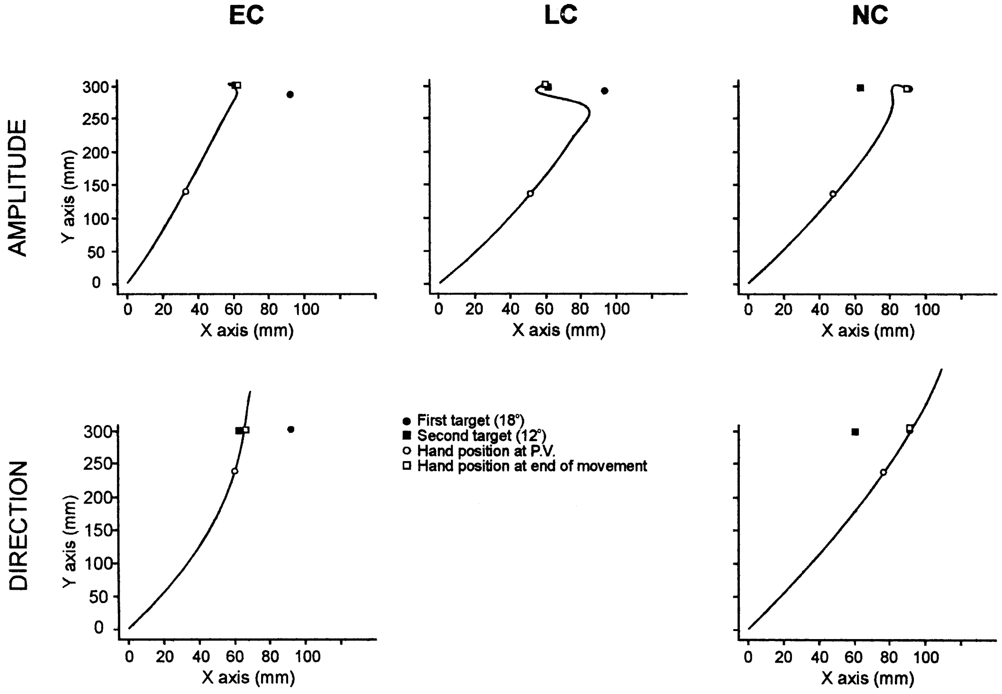

Fig. 3 Typical trajectories observed for each task in the three categories: *EC* trajectories with early corrections, *LC* trajectories with late corrections and *NC* trajectories not corrected. The percentage of trajectories found for each experimental condition is presented in Table 2. (*P.V.* Peak velocity

direction-amplitude aiming tasks (166 ms vs 114 ms). However, for directional aiming, peak velocity was reached significantly faster in darkness ($P < 0.01$).

Corrections were therefore, achieved without modifying the kinematics of the on-going motor programme. Task and environment characteristics had an effect on the time of occurrence of both peak velocity and peak acceleration. Such results suggest that, when programming an aiming movement, the central nervous system takes into account the nature of both the movement and the environment at hand, in order to optimize its final aiming accuracy.

Hand position variability

Standard deviations of directional hand positions were measured. A four-way ANOVA, 2 (Environment) × 2(Task) × 5(Target) × 2 (Moment), revealed a main effect of Target ($F_{4,72} = 7.05$, $P < 0.01$), the 18°–12° double step being more variable than the three single-step targets ($P < 0.01$). The main effect of Moment was also significant ($F_{4,18} = 31.44$, $P < 0.01$), hand direction at time to peak velocity being more variable than at the end of the movement ($P < 0.01$). Furthermore, the interaction of Task by Moment was significant ($F_{4,18} = 11.57$, $P < 0.01$). Post-hoc analyses revealed that, in the directional task, variability of aiming position was similar at peak velocity and end of movement ($P > 0.05$). However, for the direction-amplitude task, hand direction variability was significantly reduced during the deceleration phase. This was true for all targets ($P < 0.01$). Comparing terminal directions measured in the two tasks, directional aiming was significantly more variable than the aiming requiring an amplitude coding (3.2° vs 2.5°; $P < 0.01$).

As frequently described in the literature (e.g. Komilis et al. 1993; Blouin et al. 1995b), our results reveal that movements aimed at double-step targets were significantly more variable than those aimed at single-step targets. To further investigate the reason why target jump had an effect on hand-position variability, we conducted more detailed analyses on individual double-step trials. From these observations, we realized that arm trajectories varied according to three distinct categories: uncorrected, partially corrected and completely corrected. Consequently, in a second analysis, we grouped the double-step trials according to these three correction categories.

Trajectory corrections: a typological approach

For each subject, the mean directional hand position was measured for each single-step target (12°, 18° and 24°) and at both moments in time (peak velocity and end of movement). Using the corresponding standard deviations, confidence intervals for each single-step target were calculated and used as references for classification of double-step movements. Each individual double-step trial was categorized as: (1) early corrected (EC), if the accuracy at peak velocity was within the confidence interval of single-step accuracy (12° for the 18°–12° target, and 24° for the 18°–24° target); (2) late corrected (LC), if the hand position of the double-step trial fell within the 18° confidence interval at peak velocity, and within the 12° or 24° single-step confidence interval at end of movement; or (3) not corrected (NC), if the hand position of the double-step trial fell within the 18° confident interval at both peak velocity and end of movement. Figure 3 shows

Table 2 Percentages of observed trials and means of significant dependent variables for early correction (*EC*), late correction (*LC*) and no correction (*NC*). The *left section* refers to results for the amplitude-direction task, and the *right section* refers to results for the direction only task. Top results are for aimings performed in the structured environment and bottom results are for those performed in darkness. *ISA* Inter-saccadic interval; *D* Time interval between target jump and movement onset; *TPV* Time to peak velocity; *CPV* Correlation between D and directional error at peak velocity; *CEM* Correlation between D and directional error at end of movement

	Amplitude						Direction					
	%	ISA	D	TPV	CPV	CEM	%	ISA	D	TPV	CPV	CEM
Structured environment												
EC	32	196	132	106	0.16	0.24	55	319	158	212	0.04	0.02
LC	36	203	84	101	0.01	–0.31						
NC	32	317	60	99	–0.24	–0.23	45	311	77	186	–0.22	–0.30
Dark environment												
EC	43	186	172	126	–0.06	–0.25	33	252	140	141	0.16	0.34
LC	25	171	106	121	–0.77*	–0.62*						
NC	32	211	86	113	–0.22	0.23	67	234	76	146	–0.01	–0.12

* $P<0.05$

typical trajectory amendments observed in two subjects performing (a) the direction-amplitude task and (b) the directional task. Percentage of trials (collapsed across subjects) for each category, according to task and environment are presented in Table 2.

In directional aiming movements there were no trials with late corrections. Five categories were therefore used for the following statistical analyses: AEC, ALC, ANC for the direction-amplitude task, and DEC, DNC for the directional task. Taking these categories into account, we submitted all dependent variables of the first analysis to a 2 (Environment) × 5 [Category (AEC, ALC, ANC, DEC, DNC)] analyses of variance. This typology-based analysis yielded different conclusions from those previously deduced from the initial analyses, for the following variables only: intersaccadic interval (ISA), time interval between target shift and arm movement onset (i.e. the Determinant Time Interval, D) and time to peak velocity. These specific results only are discussed further.

For the ISA, the main effects of Environment ($F_{1,327} = 23.63$, $P < 0.01$) and Category ($F_{1,327} = 12.01$, $P < 0.01$) were significant. The inter-saccadic latency was longer in the structured (269 ms vs 210 ms) than in the dark environment . For the Category effect, post-hoc analyses revealed that, in both environments ($P < 0.01$), the Amplitude Early Correction (AEC) category and the Amplitude Late Correction (ALC) category were shorter than the Amplitude No Correction (ANC) category. Direction Early Correction (DEC) and Direction No Correction (DNC) categories were similar ($P > 0.05$). For the time interval between target shift and arm movement onset (D), the main effect of Category only ($F_{1,327} = 34.08$, $P < 0.01$) was significant. In both environments, AEC was significantly longer than ALC and ANC ($P < 0.01$) and DEC was longer than DNC ($P < 0.01$).

For time to peak velocity, the interaction Environment × Category was significant ($F_{4,327} = 39.36$, $P < 0.01$). For the direction-amplitude task, time to peak velocity was similar in both environments. Furthermore, time to peak velocity was not affected by trajectory amendments. In the directional task, the results revealed an effect of environment. In the structured environment, trajectory amendments significantly delayed time to reach peak velocity (186 ms vs 212 ms).

For the time interval between target jump and movement onset (D), the interaction Environment × Category was significant ($F_{4,327} = 3.11$, $P < 0.02$). For the two tasks, D was longer for the trajectories corrected at peak velocity than for the trajectories not corrected. In contrast to the directional task, the direction-amplitude task yielded longer values of D in the dark than in the structured environment.

In order to further understand the neural mechanisms subtending early hand trajectory corrections, correlations between hand movement latency and target jump (D) to hand accuracy at peak velocity and at end of movement were calculated according to our trajectory classification. Results presented in Table 2 only show significant correlations (–0.77 at peak velocity and –0.62 at the end of the movement) in the category in a dark environment.

Discussion

In the present experiment, subjects aimed at targets that were suddenly displaced. The experimental protocol did not allow conscious perception of the target displacement. Therefore, we were able to test the capacity of the central nervous system (CNS) to monitor and control on-going motor responses, without mechanically and/or cognitively perturbing the subject. The change of target location just prior to the onset of arm movement forced subjects to use available feedback signals to detect and to correct trajectory errors. Since visual feedback from the moving arm was precluded, only proprioceptive information and/or internal feedback loops (i.e. an efferent copy) could be used by the CNS to adjust the arm trajectory according to the target's new position in space.

Environment and corrective loops

When aiming towards double-step targets, the nature of the visual environment becomes determinant. Indeed, a most interesting finding is that a given visual environment not only has a different effect on direction-amplitude and directional tasks, it even determines a specific corrective strategy for each task.

For the direction-amplitude task, corrections occured earlier when movements were performed in the structured than in the unstructured environment. The structured environment was helpful for error detection and/or correction. Conversely, directional aimings were corrected more quickly in darkness than in the structured environment, which suggests that additional visual cues increased the difficulty of trajectory amendments.

The typology, which we established according to the temporal location of trajectory corrections, allowed us a more detailed view of the nature of the corrective process. The absence of correlation between D and the directional error (DE) obtained at peak velocity for early corrections (EC), both in the structured and the dark environment, supports von Sonderen's hypothesis that modification time (D) must be around 200 ms to allow the system to reprogramme the trajectory. In our study complete reprogramming took place before hand movement initiation only.

A second interesting finding is the strong D-DE correlation (–0.77) obtained at peak velocity for the ALC performed in a dark environment. This contrasts with the absence of correlation (0.01) observed for aiming movements performed in a structured environment. Our results support the hypothesis that, in a dark environment, a gradual shift of the direction of the hand from the first target to the second target (van Sonderen et al. 1988, 1989, 1990) or an averaging process (Flash 1990; Flash and Henis 1991) takes place. It is legitimate, therefore, to argue that as soon as information about the second target location has been defined, the CNS generates a trajectory plan, which is continuously added to the first plan to yield a combined trajectory (Flash 1990). However, in an exocentric frame, the subjects' corrective behavior cannot be predicted by the averaging theory. It could be hypothesized that, when the visual environment is structured, target localization should be easier, since the subject's view of spatial landmarks enables the construction of a precise visual map allowing control via peripheral proprioceptive loops. This interpretation is in agreement with the conclusion of van der Meulen et al. (1990) that both efferent and afferent information play a role in a continuous control system of arm movement. The role of the efferent copy is important when delays for corrections are short; then it can be used early in the course of the movement whereas, when enough time is available, peripheral feedback contributes to error reduction. Abbs and Gracco (1984) suggested that late activation of the lower lip elevator is based on a reprogramming triggered by proprioceptive feedback, whereas early movement of the upper lip depressor is an open-loop adjustment, which is independent of sensory feedback in the usual sense. Such a statement could be challenged by testing deafferented subjects.

It should also be mentioned that information about target location is an essential input to control goal-directed limb movements (Kalaska 1991; Gottlieb 1993). More precisely, saccade-related signals provide accurate information about eye orientation after the saccade, and hence about target direction (Blouin et al. 1995b). Furthermore, the efferent copy of the oculomotor commands is also known to provide information about eye-target positions, i.e. about the spatial goal of the arm movements to be programmed (Blouin et al. 1995b). Therefore, it could be assumed that modification of the hand program was highly related to the eye efferent copy. An experiment is in progress to test this hypothesis.

Overall, the present experiment shows that rapid aiming movements can be efficiently corrected when the target is suddenly displaced. These amendments, however, are influenced by both the task and the visual environment in which the subject is performing. Our results support the finding that, for early corrections, the delay between the target shift and arm movement onset (or von Sonderen's modification time) must be around 150 ms, allowing the system to reprogramme the trajectory. Furthermore, for late corrections we were able to identify two different kinds of trajectory corrections according to the nature of the environment (dark or structured).

In the dark environment, a significant correlation of –0.77 was obtained between modification time and directional error, emphasizing a gradual shift from the first to the second target. This supports von Sonderen's gradual shift and Flash's averaging model. Conversely, a structured environment yielded no correlation between D and and directional error, suggesting that the corrections obtained in this case were due to on-line error reductions following the new target location. These on-line corrections are most probably based on proprioceptive feedback. We are now testing this hypothesis with a deafferentation model. For amplitude aiming movements, movement duration permitted corrections to be of peripheral (i.e. proprioceptive) or central origin. When the target jump occurred just prior to movement onset, trajectories were corrected only if the target was foveated before the end of the arm movement. Since no modification of the motor programme was possible before the beginning of aiming, it could be hypothesized that corrections were of proprioceptive origin. On the other hand, early corrections were observed when target jump occurred at least 150 ms before arm movement initiation. This could constitute the minimum time needed by the CNS to use internal feedback efficiently. We suggest that an averaging of the trajectory is definitely the regulation mode adopted within an egocentric frame of reference, whereas in a structured environment, corrections could be due to online regulation based on the location of the target with respect to the proprioceptively perceived location of the arm.

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