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Visual guidance of arm reaching: Online adjustments of movement direction are impaired by amplitude control

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Most reaching arm movements have amplitude and direction constraints. Here we investigated the interdependence of these movement parameters in terms of visual control. To do so, we asked human adults to look and reach toward targets such that, in a first experiment, both movement amplitude and direction had to be controlled. Randomly, hand visual feedback was shifted near arm movement onset to influence movement direction, movement amplitude or both. Because the visual shifts occurred during ocular saccades, they were not consciously perceived. The rapid reaching movements (mean duration = 334 ms) were slightly influenced by the visual shifts (approximately 15% and 8% of visual adjustment for movement direction and amplitude, respectively). Moreover, directional adjustments varied according to amplitude adjustments (and vice-versa). We thus examined, in a second experiment, the effect of relaxing the requirement to control movement amplitude. Asking participants to control only movement direction led to substantial directional adjustments (49%) based on shifted hand visual feedback. Overall, these findings indicate that the control of movement amplitude constrains the online adjustments of movement direction and that the mechanisms controlling movement amplitude and direction are not independent.

Keywords: visuo-motor transformations, feedback control, manual aiming, movement extent and direction

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Introduction

Vision is a major source of information in human motor control. Not only vision informs us about the environment but it also provides feedback about our body configuration. When considering reaching arm movements for instance, visual feedback of the moving hand is an important source of information to guide the hand toward the goal-target (Brenner & Smeets, 2003; Carlton, 1981; Elliott & Allard, 1985; Franklin & Wolpert, 2008; Jakobson & Goodale, 1989; Khan et al., 2006; Proteau, Roujoula, & Messier, 2009; Sarlegna et al., 2004; Saunders & Knill, 2004). Reaching movements can thus be adjusted online when an error in movement trajectory is detected, provided that task constraints such as movement duration are not too stringent (Elliott, Binsted, & Heath, 1999; Liu & Todorov, 2007; Woodworth, 1899).

When reaching for a visual target, the hand path is generally straight (Morasso, 1981). Therefore, reaching movements are often described as vectors defined in terms of direction and amplitude (Desmurget, Pélisson, Rossetti, & Prablanc, 1998). The planning of movement direction and amplitude has been shown to rely on distinct

mechanisms (Rosenbaum, 1980; Sainburg, Lateiner, Latash, & Bagesteiro, 2003), an idea further supported by neurophysiological findings (Desmurget, Grafton, Vindras, Gréa, & Turner, 2004; Fu, Flament, Coltz, & Ebner, 1995; Messier & Kalaska, 2000; Riehle & Requin, 1989). The difference in amplitude and direction control is also well reflected by final position errors, which are generally larger in amplitude than in direction (Gordon, Ghilardi, & Ghez, 1994; Soechting & Flanders, 1989).

Because it is common for humans to look at the target just before reaching it (Biguer, Jeannerod, & Prablanc, 1982; Saunders & Knill, 2003; Vercher, Magenes, Prablanc, & Gauthier, 1994), the hand's visual image generally sweeps the peripheral retina in the early phase of the reach. Peripheral vision has been shown to allow rapid adjustments of movement direction (Bard, Hay, & Fleury, 1985; Blouin, Teasdale, Bard, & Fleury, 1993; Paillard, 1996; Proteau, Boivin, Linossier, & Abahnini, 2000; Sarlegna et al., 2004). The early foveation of the target also implies that the hand appears in the central visual field toward the end of the reach. Such central visual feedback allows adjustments in movement amplitude during the late phase of the reach, according to several studies (Bard, Paillard, Fleury, Hay, & Larue,

1990; Lawrence, Khan, Buckolz, & Oldham, 2006; Sarlegna et al., 2003). Recent studies demonstrated that central vision is also useful for the online control of movement direction (Proteau et al., 2009; Saunders & Knill, 2003, 2004). In fact, Bédard and Proteau (2004) suggested that both the peripheral and central retina are apt at detecting on-line amplitude and direction errors in movements lasting more than 400 ms. This was supported by a study of Saunders and Knill (2005), who showed that both movement amplitude and direction could be rapidly adjusted based on hand visual feedback (slight differences were found in response latencies but these could be attributed to differences in perceptual sensitivity). On the other hand, several studies reported that peripheral vision does not contribute to the online control of movement amplitude (Bard et al., 1990; Blouin et al., 1993; Lawrence et al., 2006). Such findings may indicate that distinct visual mechanisms underlie the online control of movement amplitude and direction.

To date, an unresolved issue concerns the interaction between the visual control of movement amplitude and direction. The goal of the present study was to uncover the independence, or interdependence, of these feedback control mechanisms. An original feature of the present study was that, in [Experiment 1](#), hand visual feedback was shifted such that, in order to bring the seen hand on the target, participants had to adjust movement amplitude, movement direction or both. Therefore, the experimental protocol enabled us to determine whether hand visual feedback differently contributes to the regulation of movement amplitude and direction but also whether there are interaction effects. If the online adjustments of movement amplitude and direction rely on fully independent processes, there should be no interaction. However, it is possible that having to adjust both movement amplitude and direction may result in a general decrease of online adjustments.

Previous work suggests that the need, for task performance, to precisely control movement amplitude impairs the online control of movement direction. This idea stems from the observation that online adjustments in response to a sudden target displacement are smaller when participants have to stop on the target than when amplitude requirements are relaxed (i.e., reach-and-stop vs. shooting movements: Blouin, Bridgeman, Teasdale, Bard, & Fleury, 1995a; Blouin, Teasdale, Bard, & Fleury, 1995b). Recently, Liu and Todorov (2007) provided additional support for the idea that the online control of goal-directed arm movements is strongly influenced by the deceleration requirements of the task. Liu and Todorov (2007) showed that when the hand has to stop on the target, movement control becomes less sensitive to positional errors (artificially induced in their study with sudden target displacements) as it is getting more concerned with stopping the movement in a stable manner. The authors reasoned that if the gain between positional errors and motor responses remained high toward

movement end, this would cause terminal oscillations conflicting with the requirement to stop. Liu and Todorov (2007) thus suggested that the central nervous system achieves endpoint stability while compromising its ability to correct for final errors. They tested their idea of a trade-off between stability and positional accuracy by varying the stopping requirement in a second experiment. Liu and Todorov (2007) found that online adjustments in response to a target displacement were greater in the shoot condition than in the reach-and-stop condition. However, all these findings were observed while vision of the hand was not available. Given that hand visual feedback substantially contributes to the online control of reaching movements, notably by facilitating the corrective adjustments of arm trajectory in response to target displacements (Reichenbach, Thielscher, Peer, Bulthoff, & Bresciani, 2009; Sarlegna et al., 2003), task constraints such as the requirement to control movement amplitude may not affect motor performance when hand visual feedback is available. We thus performed a second experiment in which participants had to control only movement direction for task performance to directly test the hypothesis that the control of movement amplitude constrains the guidance of movement direction based on hand visual feedback. This hypothesis predicts that shooting movements, which can be adjusted based on hand visual feedback even when they are very rapid (Bard et al., 1985; Blouin et al., 1993; Khan, Lawrence, Franks, & Buckolz, 2004; Proteau et al., 2000; Sarlegna et al., 2004), should be adjusted more efficiently than reach-and-stop movements.

In the present study, we introduced shifts in hand visual feedback in randomly selected trials, during the saccadic eye movements toward the goal target. Because of the saccadic suppression phenomenon (Bridgeman, Lewis, Heit, & Nagle, 1979; Wurtz, 2008), participants did not consciously perceive the visual shift (Goodale, Péllisson, & Prablanc, 1986; Sarlegna et al., 2003). Therefore, our protocol enabled us to discard the influence of cognitive and offline, adaptive strategies on the visual guidance of reaching movements.

Experiment 1—Reaching movements (stop on target)

Methods

Subjects

Eight self-declared right-handed males (mean age = 25 years) participated to [Experiment 1](#). They all gave informed consent prior to the study, according to University regulations and the 1964 Declaration of Helsinki. All participants were naïve concerning the goal of the present study. They all reported normal vision and no known sensori-motor impairment.

Experimental set-up

A schematic representation of the apparatus is shown in [Figure 1A](#). Participants were seated in complete darkness. A U-shaped restraint was used to prevent head movements. Two light-emitting diodes (LEDs, 3 mm in diameter) were fixed above a horizontal semi-reflecting

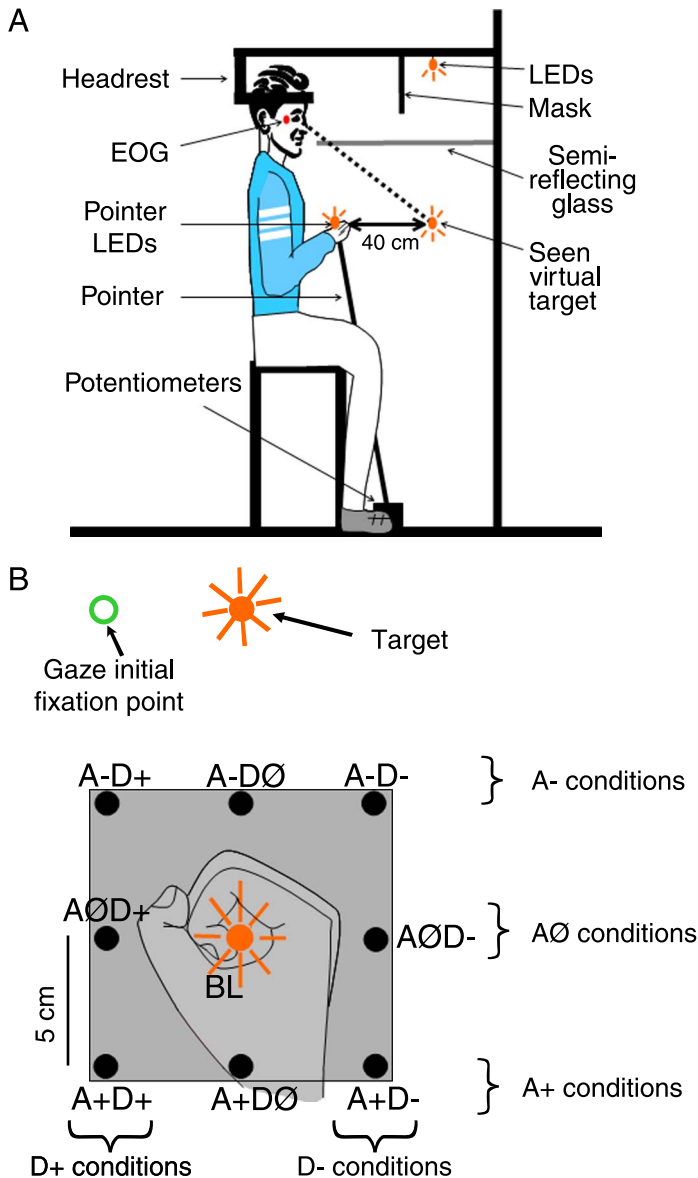


Figure 1. Experimental set-up **A** Side view **B** Top view of the nine LEDs used to provide true or erroneous visual feedback of hand position in complete darkness. Only one LED was lit at a time. The central LED was always lit at the beginning of the trial. The initial fixation point and the target are also presented but, for purpose of illustration, distances are not scaled properly (see [Methods](#)). In D+ conditions, movement trajectory had to be adjusted rightward to bring the seen hand on the target. In A+ conditions, movement amplitude had to be increased to bring the seen hand on the target. Note that at target level, 5 cm corresponded to 6°.

glass, which was positioned at chin level. A panel prevented direct vision of the LEDs: participants could only see their virtual images beneath the glass, in the hand workspace. The virtual image of an orange LED positioned straight-ahead (0°) was used as the target. It was located 40 cm away from the hand starting position, indicated by a notch in a metal bar. The virtual image of a green LED located at 24° to the left (−24° relative to the cyclopean eye) served as the gaze fixation point.

Participants were asked to reach with their right hand toward the target while holding a pointer. Since no contact was possible with the virtual target, participants had to actively and fully control movement amplitude. Such precise control of movement amplitude is necessary in several natural movements such as when grasping a fragile object (e.g., raspberry) or a full cup without spilling its content. The pointer consisted of a light, quasi-frictionless rod. Visual feedback about hand position was provided using 9 orange LEDs fixed on the upper end of the pointer. As shown in [Figure 1B](#), one LED was aligned with the rod and provided veridical information about hand position. The other LEDs were spaced around the central LED to provide erroneous visual feedback of hand position: relative to the central LED, LEDs were positioned 5-cm leftward, 5-cm rightward, 5-cm upward, 5-cm downward, 5-cm upward and leftward, 5-cm upward and rightward, 5-cm downward and leftward and 5-cm downward and rightward. Two potentiometers, perpendicularly fixed at the rod base, were used to measure pointer movements in the lateral (x coordinate) and antero-posterior (y coordinate) planes. Signals from the potentiometers were sampled at 500 Hz with a 12-bit analog/digital card (measured spatial accuracy <1 mm). Horizontal eye movements were monitored at 500 Hz by mean of DC electro-oculography with conventional bio-isolated amplifiers (Lablinc V marketed by Coulbourn). Small silver–silver chloride surface electrodes (10 mm in diameter) were fixed near the outer canthi of the eyes and a ground electrode was placed on the forehead. The experiment was controlled by means of a real-time acquisition system ADwin-Pro (Jäger, Germany), a computer and customized software.

Procedure—Experimental conditions

Each trial started with the illumination of the central pointer LED and the fixation point for 1.5 s during which participants had to look at the fixation point. After this delay, the fixation point was switched off and the visual target was switched on. Participants had then to produce a saccadic eye movement toward the target and to reach it with the hand. Because the participants' task was to stop the hand beneath the virtual target, they had to control both the amplitude and the direction of their movements. Participants had to maintain final hand position until the end of the trial, when all LEDs were switched off (3 s after trial onset).

In some trials, at peak velocity of the ocular saccade (i.e., during the saccadic suppression of displacement; Bridgeman et al., 1979), the central pointer LED was switched off whereas another LED was lit. The central pointer LED could also remain lit throughout the trial (baseline trial (BL)). Figure 1B shows which LED was used in each experimental condition after the peak velocity of the saccade. Different adjustments of hand trajectory were expected for each condition, i.e., each hand visual feedback. For instance, in AØD+ conditions, the shift of hand visual feedback did not require any amplitude adjustments (relative to the planned trajectory and the trajectory in BL condition) but hand trajectory had to be deviated to the right in order to bring the seen hand on the target. In A–DØ conditions, participants only had to reduce movement amplitude by 5 cm. The other conditions required a combination of direction and amplitude adjustments (see Figure 1B).

Participants were asked to produce rapid arm movements toward the target. They were trained to perform movements in approximately 350 ms. However, movement duration was not constrained within a certain range during the experiment to let arise possible differences between experimental conditions on this dependant variable. Participants were also asked to synchronize the best they could eye and arm movement onsets. A few BL trials were used as practice, allowing participants to comply with these instructions. However, when the latency between arm and eye movements' onsets was greater than 130 ms during the experimental session, the trial was rejected and repeated later to ensure that the shifts in hand visual feedback occurred near arm movement onset.

The order of presentation of the experimental conditions was pseudo-randomly selected with the restriction that trials involving a shift in hand visual feedback were always preceded by a trial without any shift in hand visual feedback. This minimized the influence of offline adaptive processes since visual error signals, especially when repeated over consecutive trials, can be used to update visuo-motor transformations in subsequent trials (Held & Freedman, 1963; Khan et al., 2006; Sarlegna, Gauthier, & Blouin, 2007). Because the baseline trials (without shift in hand visual feedback) may also have been influenced by such adaptive control, we analyzed only those trials which were not preceded by a trial with a shift in hand visual feedback. Trials were ordered to yield eight trials per condition for data analysis. Each participant completed 137 trials, 64 of those involving a shift in hand visual feedback (i.e., 47% of perturbed trials).

Data analysis

Signals were filtered with a low-pass Butterworth filter (7th order, 10 Hz cut-off frequency). The main measured parameters were arm movement amplitude and direction.

Movement amplitude was defined as the 2D distance between starting hand position and actual hand position. Hand direction was defined as the direction of the hand relative to the cyclopean eye; straight-ahead was 0° and negative/positive values were assigned to hand direction when the hand was to the left and to the right of the target, respectively. Movement onset was determined when tangential hand velocity reached 5 cm/s. Offline analyses showed that reaching movements consisted in a primary movement and a secondary, stabilization phase (with one or multiple corrective movements). We computed movement amplitude and direction at the end of the primary movement (movement offset), i.e., when hand velocity first dropped under 5 cm/s after peak velocity. Movement amplitude and direction were also measured at peak velocity and peak deceleration.

The normality of data sets was verified using the Kolmogorov–Smirnov method. The main statistical analyses consisted in 3×3 [Amplitude (A+, AØ, A–) \times Direction (D+, DØ, D–)] analyses of variance (ANOVA) with repeated measures. Significant effects were further analyzed using post-hoc, Tukey HSD tests which take into account the number of means being compared. A 0.05 significance threshold was used for all analyses.

Results

None of the participants reported perceiving a shift in hand visual feedback. However, participants did perceive that their reaching movements were frequently inaccurate. When asked for general comments at the end of the experiment, some participants reported having felt differences in terminal arm postures across trials and attributed this to the use of different targets (instead of a shift in hand visual feedback). On average, the shifts in hand visual feedback occurred 52 ms before arm movement onset. This delay did not significantly vary across the experimental conditions ($F_{7,49} = 1.0$; $P = 0.46$). A latency of ~50 ms being too short to fully plan a new movement (Georgopoulos, Kalaska, & Massey, 1981; van Sonderen, Denier van der Gon, & Gielen, 1988), online adjustments of the hand trajectory during movement execution were necessary to bring the seen hand on the target.

Small directional adjustments based on hand visual feedback during the rapid movements

Figure 2 shows representative hand paths in each experimental condition for a single participant. Apparent is the fact that the participant tended to bring directly the hand to the target and performed late, small adjustments of the rapid hand movements based on the shifted hand visual feedback; in a secondary corrective phase, he displaced the hand according to the visual shift.

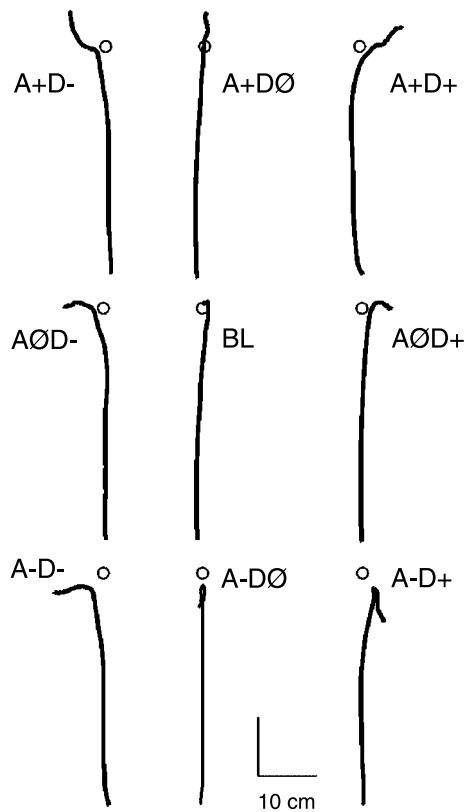


Figure 2. Top view of representative spatial paths of the hand (i.e., not of the lit pointer LED) in the reach-and-stop movements. Note that all movements actually started from the same starting position.

Figure 3A shows that, on average across subjects, there were small adjustments of hand direction at the end of the primary movement in response to the shifts in hand visual feedback. When the shifts in hand visual feedback required leftward adjustments of movement trajectory ('D- conditions'; see Figure 1B) in order to bring the seen hand on the target, hand direction was adjusted leftward relative to the conditions which did not require directional adjustments (DØ conditions). Conversely, hand direction was adjusted rightward when the shifts in hand visual feedback required so (D+ conditions). These adjustments were statistically significant, as shown by a 3×3 [Amplitude (A+, AØ, A-) \times Direction (D+, DØ, D-)] ANOVA on hand direction at movement offset. This analysis revealed that hand direction was significantly affected by the factor Direction ($F_{2,14} = 51.4$; $P < 0.001$). The ANOVA on hand direction did not show a significant effect of the Amplitude factor ($F_{2,14} = 0.1$, $P = 0.92$) but revealed a significant Amplitude \times Direction interaction ($F_{4,28} = 2.9$; $P < 0.05$). Post-hoc analysis of the interaction showed that hand direction differed between A-D-, A-DØ and A-D+ conditions (means = -0.4 , 1.0 and 2.5° , respectively; all P s < 0.05), i.e., within conditions requiring an amplitude reduction. In contrast, in conditions requiring an amplitude increase (A+ conditions),

hand direction only differed between A+D- condition (mean = 0.5°) and A+D+ condition (mean = 1.8° ; $P < 0.05$). Also, in AØ conditions, hand direction only differed between AØD- condition (mean = 0.4°) and AØD+ condition (mean = 2.0° ; $P < 0.01$). Therefore, the analysis of the interaction shows that the requirement to adjust movement amplitude impacted hand direction.

We investigated whether the directional adjustments were quantitatively similar in all conditions requiring rightward or leftward adjustments (D+ and D- conditions, respectively). For each participant, we computed the absolute values of directional adjustments relative to the BL condition. A 2×3 [Direction (D+, D-) \times Amplitude (A+, AØ, A-)] ANOVA did not reveal any significant effect (all P s > 0.05). On average, arm movements were adjusted by 1.0° relative to the BL condition, a value corresponding to only 16% of the required 6° adjustment to bring the seen hand on the target.

An Amplitude \times Direction ANOVA showed that hand direction variability (standard deviation of the mean) was affected by the Direction factor ($F_{2,14} = 8.1$). Hand direction was less variable in conditions which did not require directional adjustments (DØ conditions; mean = 1.5°) than in conditions requiring directional adjustments (mean of D- and D+ conditions = 2.0 and 2.1° , respectively; $P < 0.05$ and 0.01). This increased variability

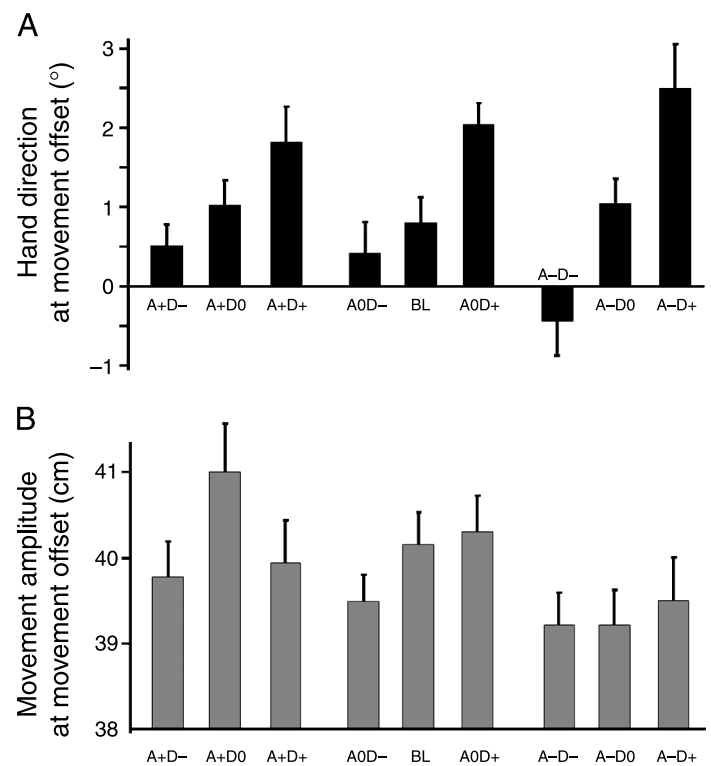


Figure 3. Direction and amplitude of reach-and-stop movements **A**. Hand direction at the end of the primary movement (movement offset). Vertical bars represent the standard error. **B**. Movement amplitude at movement offset. Vertical bars represent the standard error.

likely stems from the ongoing corrective adjustments. There was no significant Amplitude ($F_{2,14} = 1.6$; $P = 0.23$) or interaction effect ($F_{4,28} = 0.3$; $P = 0.87$).

Small amplitude adjustments based on hand visual feedback during the rapid movements

Figure 3B shows that movement amplitude at the end of the primary movement was slightly adjusted based on the shifts in hand visual feedback. Movements performed in conditions requiring a reduction in movement amplitude to bring the seen hand on target ('A− conditions') were shorter than those which did not require an amplitude adjustment. The mean 0.7 cm amplitude reduction in A− conditions corresponded to only 14% of the 5 cm shift in hand visual feedback. Significant effects of the Amplitude factor ($F_{2,14} = 14.7$; $P < 0.001$) and Direction factor ($F_{2,14} = 6.0$; $P < 0.05$) were found on movement amplitude. The significant interaction ($F_{4,28} = 4.6$; $P < 0.01$) revealed that movement amplitude tended to be increased, relative to the BL condition (mean = 40.2 cm; $P = 0.09$), only when no directional adjustments were required. Indeed, amplitude was greater in A+DØ condition (mean = 41.0 cm) than in A+D− and A+D+ conditions (mean = 39.8 and 39.9 cm; $P < 0.01$ and 0.05, respectively). On the other hand, there were no significant differences in amplitude within AØ conditions and within A− conditions. Movement amplitude was shorter in A−DØ (mean = 39.2 cm) and A−D− (mean = 39.2 cm) conditions than in the BL condition (both P s < 0.05).

The ANOVA performed on the final variability of movement amplitude revealed a significant effect of the Amplitude factor ($F_{2,14} = 4.7$; $P < 0.05$), movement amplitude being less variable in A− conditions (mean = 1.5 cm) than in A+ conditions (mean = 2.0 cm; $P < 0.05$). The effect of the Direction factor was not significant ($F_{2,14} = 0.8$; $P = 0.45$) but the interaction was significant ($F_{4,28} = 4.2$; $P < 0.01$). Post-hoc analysis revealed that amplitude variability in the BL condition was lower than that in AØD− and all A+ conditions (all P s < 0.05) but did not significantly differ from that in AØD+ and all A− conditions.

Kinematic analyses reveal late adjustments of the rapid reaching movements

Movement duration was modified when the shift in hand visual feedback required an amplitude adjustment ($F_{2,14} = 13.6$; $P < 0.001$). Duration of the primary movement was shorter when a reduction of movement amplitude was required (mean = 309 ms) than when an increase (mean = 355 ms; $p < 0.001$) or no adjustment of movement amplitude was required (mean = 337 ms; $p < 0.05$). Movement duration was also modified when the shift in hand visual feedback required a directional adjustment ($F_{2,14} = 14.8$; $P < 0.001$). Movement duration was shorter when a rightward or leftward adjustment was

required (mean = 333 and 319 ms, respectively) than when no directional adjustment was required (mean = 348 ms; all P s < 0.05). There was no significant Amplitude × Direction interaction effect ($F_{4,28} = 2.4$; $P = 0.08$).

To determine whether longer movement duration allowed greater adjustments based on shifted hand visual feedback, hand direction and movement amplitude were plotted against the corresponding movement duration. For hand direction, R^2 values of the linear regression ranged between 0.32 and 0.71 (mean = 0.54) across experimental conditions, indicating that directional adjustments slightly increased with movement duration (all P s < 0.001). Adjustments in movement amplitude also increased with movement duration, R^2 values ranging between 0.32 and 0.67 (mean = 0.56) across experimental conditions (all P s < 0.001).

Figure 4 and Table 1 show the results of the analyses of movement amplitude and direction at peak velocity and peak deceleration. Because no significant effects of the experimental factors were observed, these analyses, combined with those showing significant effects at movement offset, indicate that movement amplitude and direction were adjusted online in the late stages of the deceleration phase. This view is supported by the analysis of the duration between peak deceleration and movement

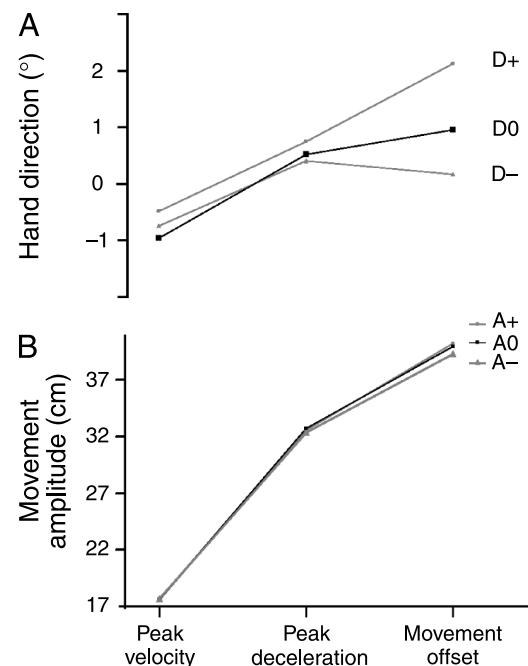


Figure 4. Time course of hand direction and movement amplitude **A**. Time course of hand direction, averaged across conditions requiring leftward adjustments (D− conditions), no adjustments (D0 conditions) or rightward adjustments (D+ conditions) of movement trajectory to bring the seen hand on the target. **B**. Time course of movement amplitude averaged across conditions requiring a reduction (A− conditions), no adjustments (A0 conditions) or an increase (A+ conditions) of movement amplitude to bring the seen hand on the target.

Time to peak velocity	128 ms	No significant main or interaction effect
Peak velocity	2.8 m/s	No significant main or interaction effect
Mean amplitude at peak velocity	17.6 cm	No significant main or interaction effect
Amplitude variability at peak velocity	1.6 cm	No significant main or interaction effect
Mean hand direction at peak velocity	−0.7°	No significant main or interaction effect
Direction variability at peak velocity	2.5°	No significant main or interaction effect
Time to peak deceleration	192 ms	No significant main or interaction effect
Peak deceleration	−28.2 m/s/s	No significant main or interaction effect
Mean amplitude at peak deceleration	32.6 cm	No significant main or interaction effect
Mean hand direction at peak deceleration	0.6°	No significant main or interaction effect
Direction variability at peak deceleration	2.2°	No significant main or interaction effect

Table 1. Mean value and summary of 3×3 ANOVA for various kinematic parameters.

offset. Such duration varied when amplitude had to be adjusted ($F_{2,14} = 11.9$; $P < 0.001$) as it was shorter in A− conditions (mean = 118 ms) than in A+ conditions (mean = 164 ms; $P < 0.001$). This duration also varied when direction had to be adjusted ($F_{2,14} = 15.0$; $P < 0.001$) as it was shorter in D− conditions (mean = 125 ms) than in DØ and D+ conditions (mean = 156 and 143 ms; $P < 0.001$ and 0.05 , respectively). There was no significant interaction ($F_{4,28} = 2.0$; $P = 0.12$).

Experiment 2—Shooting movements (no stopping on target)

In [Experiment 1](#), we asked participants to stop on the target and we observed small online adjustments of movement trajectory, even when only movement direction had to be adjusted (i.e., AØD+ and AØD− conditions). This strikingly differed from the online adjustments observed in a previous study (Sarlegna et al., 2004) in which participants only had to control movement direction for task performance (participants were asked to pass through the virtual target and stretch out the arm to full extension). Adjustments of movement trajectory were observed after approximately 150 ms such that 45% of the shift in hand visual feedback was eventually taken into account. To determine whether similar adjustments would be observed in the context of the present study, we asked five different, naïve right-handed males (mean age = 22 years) to participate in a second experiment.

The set-up and procedure were identical to [Experiment 1](#) except that participants were instructed to pass through the target until full arm extension, i.e., to precisely control the direction of their movement. Because there was no amplitude constraint in this task except that the hand had to cross the target plane, experimental conditions involving

an adjustment of movement amplitude in [Experiment 1](#) were not used. Therefore, only AØD−, AØD+ and BL conditions were used. We will refer to these as D−, D+ and BL conditions since directional control was emphasized in this second experiment. All participants had normal (or corrected to normal) vision and reported no known pathology. Each participant completed 40 trials, 16 involving a shift in hand visual feedback (i.e., 40% of perturbed trials).

We explicitly informed participants that movement accuracy was determined at target level. Indeed, hand direction was determined when the hand crossed the fronto-parallel plane of the target. Because movement duration affects final accuracy (Fitts & Peterson, 1964; Keele & Posner, 1968; Saunders & Knill, 2003), we trained participants to perform movements in approximately 350 ms as in the first experiment. It should be noted that while movement duration and mean velocity matched those of [Experiment 1](#), peak velocity was higher in [Experiment 1](#) than in [Experiment 2](#) because of different task constraints (respectively 2.8 m/s and 1.6 m/s as shown by off-line analyses). However, several studies have shown that online adjustments of movement trajectory can be made for movements whose peak velocity exceeds 2 m/s (e.g., Boulinguez & Nougier, 1999; Flanagan, Ostry, & Feldman, 1993; Turrell, Bard, Fleury, Teasdale, & Martin, 1998). Thus, we preferred similar movement durations (~350 ms) in both experiments rather than similar peak velocities, as the latter option would have yielded large differences in movement durations.

Results

On average, shifts in hand visual feedback occurred 27 ms before arm movement onset. A t-test for paired samples showed that the latency between the visual shift and arm movement onset did not differ between D+ and D− conditions ($t = 0.1$; $P = 0.96$).

[Figure 5A](#) shows movement trajectories in the 3 experimental conditions. The rapid, shooting movements were

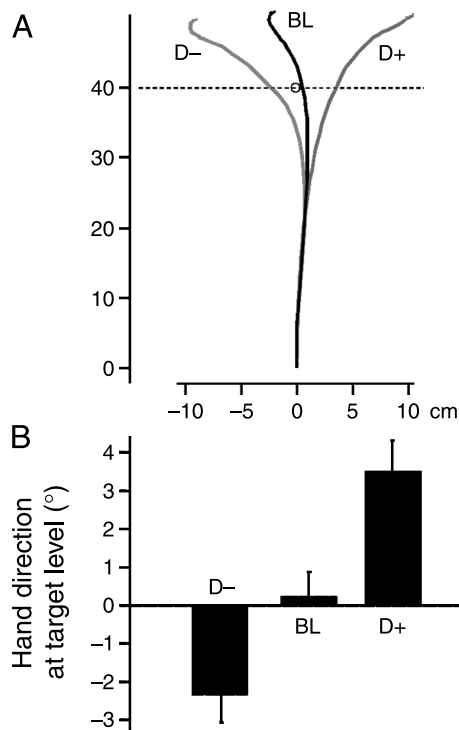


Figure 5. Direction of shooting movements **A**. Mean spatial hand paths of the shooting movements performed by a representative participant (top view). **B**. Hand direction at target level. In D- conditions, movement trajectory had to be adjusted rightward to bring the seen hand on the target. Vertical bars represent the standard error.

accurate in the BL condition but more importantly, substantial online adjustments were observed in both D- and D+ conditions. An ANOVA revealed that the shifts in hand visual feedback significantly affected hand direction at target level ($F_{2,8} = 49.1$; $P < 0.001$). Post-hoc analysis showed that hand direction in D- condition (mean = -2.3°) differed from that in BL condition (mean = 0.2° ; $P < 0.01$) which in turn differed from that in D+ condition (mean = 3.5° ; $P = 0.001$). A t-test performed on the absolute values of directional adjustments in D+ and D- conditions (Figure 5B) showed no significant difference ($t = 1.4$; $P = 0.23$). In these conditions, hand direction was adjusted by 2.9° on average, a value corresponding to 49% of the required 6° adjustment at target level.

The visual shifts did not significantly affect the variability of hand direction at target level (mean = 1.6° ; $F_{2,8} = 1.2$; $P = 0.35$). Movement duration, defined as the duration between movement onset and the time the hand crossed the target plane, averaged 364 ms and was not significantly influenced by the visual shifts ($F_{2,8} = 1.3$; $P = 0.33$). When hand direction was plotted against the corresponding movement duration, R^2 values of the linear regression were 0.30 and 0.15 in D+ and D- conditions, respectively, indicating that directional adjustments slightly increased with movement duration ($P < 0.001$ and 0.05, respectively).

There was no significant effect of the experimental condition on mean hand direction measured at peak velocity when considering its mean (mean = 0.0° ; $F_{2,8} = 3.1$; $P = 0.10$) and its variability (mean = 2.0° ; $F_{2,8} = 0.5$; $P = 0.62$). Peak velocity occurred 227 ms after movement onset on average and was not significantly influenced by the shifts in hand visual feedback when considering its timing ($F_{2,8} = 2.5$; $P = 0.14$) and its magnitude (1.6 m/s on average; $F_{2,8} = 2.2$; $P = 0.18$).

Discussion

In the first experiment, participants had to perform reach-and-stop movements and only small and late adjustments of movement amplitude and direction were observed at the end of the primary movement. Such effect of hand visual feedback on the amplitude of rapid reaching movements confirms previous findings (Sarlegna et al., 2003; Saunders & Knill, 2005; Smith & Bowen, 1980) and suggests that hand visual feedback contributes to the online control of movement amplitude in addition to proprioceptive feedback mechanisms (Bagesteiro, Sarlegna, & Sainburg, 2006; Reichenbach et al., 2009; Veilleux & Proteau, 2009) and target visual information (Brenner & Smeets, 2003; Danion & Sarlegna, 2007; Elliott et al., 1999; Georgopoulos et al., 1981; Goodale et al., 1986). However, the small directional adjustments observed for the reach-and-stop movements strikingly contrasted with the large adjustments found when the stop requirement was relaxed, i.e., when participants were asked to “pass through” the target. The present study thus appears to indicate that, during rapid reaching movements, the necessity to control movement amplitude impairs the ability to use hand visual feedback for the adjustment of movement direction.

To study the visual control of movement amplitude and direction, we randomly introduced shifts in hand visual feedback such that, in Experiment 1, participants had to adjust in flight movement amplitude, movement direction or both in order to bring the seen hand to the target. Results showed significant main effects of the visual shifts which required adjustments in movement direction or amplitude. Thus, both the direction and the amplitude of the rapid movements could be slightly adjusted online based on hand visual feedback. Nevertheless, the significant interaction effects found on both movement amplitude and direction suggest that movement amplitude and direction are controlled through distinct but not fully independent mechanisms (Favilla, Hening, & Ghez, 1989). This hypothesis is consistent with the fact that motor commands are sent to muscles whose activation will necessarily affect both movement amplitude and direction at the hand level. Additional evidence for the interdependence between amplitude and direction control processes comes from the fact that, because limb inertia is

anisotropic (Gordon, Ghilardi, Cooper, & Ghez, 1994), movements of the same amplitude needs to be adjusted to movement direction, for instance by reducing movement duration in directions corresponding to low inertial resistance. However, the present experiment does not allow determining whether movement amplitude and direction are controlled through distinct or common visual feedback loops. Indeed, a second possibility is that the interactions arise because visual feedback mechanisms are common for direction and amplitude control. Assuming that such feedback control mechanism has a limited capacity, one may view our findings as evidence that adjusting two parameters (i.e., movement amplitude and direction in [Experiment 1](#)) was more difficult for the visual feedback mechanisms than adjusting a single parameter (i.e., movement direction in [Experiment 2](#)).

To further test the interaction between amplitude control and direction control, we varied task requirements which are known to strongly influence feedback control processes (Bard et al., 1990; Liu & Todorov, 2007). In [Experiment 1](#), when participants had to stop on the target and thus had to precisely control movement amplitude, only about 15% of the shift in hand visual feedback was taken into account to adjust the direction of the rapid reaching movement. In [Experiment 2](#), when the stop requirement was relaxed as participants were asked to pass through the target (within a time similar to that in [Experiment 1](#)), the adjustments of movement direction increased to 49% of the visual shift, a value close to the 45% value reported in a previous, similar study (Sarlegna et al., 2004). The comparison of shooting and reach-and-stop movements suggests that the requirement to control movement amplitude limits the visual adjustments of movement direction, another argument for the claim that the neural mechanisms underlying amplitude control and direction control are not fully independent.

Our findings appear to extend previous work highlighting the influence of task constraints on online motor control, which was mainly assessed by using a target-displacement paradigm (Liu & Todorov, 2007). While movements were not particularly rapid in Liu and Todorov (600 to 900 ms), their findings are remarkably consistent with previous studies on fast arm movements (Blouin et al., 1995a, 1995b; Turrell et al., 1998). Indeed, Blouin et al. (1995a) observed large directional adjustments toward the displaced target when participants only had to control the direction of shooting, rapid movements (duration of ~200 ms). In contrast, when participants had to control both the direction and amplitude of similarly rapid movements, Blouin et al. (1995b) did not observe significant online corrections and suggested that the control of movement amplitude interferes with the control of movement direction. In summary, previous studies which employed a double-step paradigm showed that visual signals (related to target position) lead to different arm trajectory adjustments when task requirements vary. In the present study, we show that the processing of visual

signals related to hand position is influenced by the requirement to control movement amplitude. One possibility to further test whether deceleration constraints affect the visual guidance of arm movements would be to perform reaching movements, with similar movement duration and peak velocity, toward the same physical target but with varying desired impact forces. According to the present findings, one could predict that the size of the visually guided adjustments would increase as a function of the impact force.

As pointed out by Bard et al. (1985), the necessity to stop the hand on a target requires the precise control of movement amplitude by closely monitoring the braking phase and the final adjustments of the reach. Such complex control of movement deceleration has been shown to affect endpoint variability (Teasdale & Schmidt, 1991). The present findings suggest that the complexity of the control processes underlying reach-and-stop movements also impairs the visual adjustments of reaching movements, an effect which would be evident for rapid movements like those studied here but not for slower movements. Indeed, correlation analyses revealed that the size of the visual adjustments slightly but significantly increased with movement duration, a finding consistent with the known importance of movement duration for the online control of reaching (Fitts & Peterson, 1964; Keele & Posner, 1968; Khan et al., 2006; Woodworth, 1899; Zelaznik, Hawkins, & Kisselburgh, 1983). Similar, low coefficients of determination (i.e., R^2) were also found in a previous study (Sarlegna et al., 2004) investigating the visual control of shooting movements. However, the influence of movement duration on visually guided corrective responses was better evidenced by Saunders and Knill (2003, 2005) who specifically manipulated movement duration and showed that the size of the visual adjustments increased with movement duration. Differences in movement duration between the present study and those of Saunders and Knill (2003, 2005) likely explain the small adjustments reported here relative to theirs. Indeed, the reach-and-stop movements that we studied (approximately 40 cm in 330 ms) were considerably faster than those studied by Saunders and Knill (2003, 2005; approximately 25 cm movements in 450 to 600 ms).

We also would like to suggest that visually guided adjustments differ between shooting and reach-and-stop movements because similar final errors do not correspond to similar ‘costs’ for the two types of movements. When performing shooting movements, final errors may seem costly because they cannot be corrected, thus emphasizing the importance of online control mechanisms. On the other hand, one advantage of reach-and-stop movements is that the motor plan (i.e., feedforward mechanisms) is generally efficient to guide the hand in the vicinity of the target (Ingram et al., 2000; Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006), thanks to the adaptive mechanisms constantly updating sensori-motor transformations (Held & Freedman, 1963; Sarlegna et al., 2007).

Because of the efficiency of feedforward mechanisms, online adjustments of reach-and-stop movements appear to be less crucial for movement accuracy, as only small adjustments would be required to bring the seen hand exactly on target. Such factors may contribute to the differences reported here between shooting and reach-and-stop movements.

Conclusion

The present study shows that the processing of visual signals about hand position for arm motor control varies according to various task constraints. Indeed, we found that hand visual feedback was increasingly taken into account to adjust the trajectory of rapid reaching movements as movement duration increased. We also found that hand visual feedback was rapidly taken into account to adjust the direction of rapid reaching movements when movement amplitude did not have to be controlled. However, when participants had to stop on the target and thus had to control movement amplitude, visually guided adjustments were small and occurred late, presumably because the central nervous system was more concerned about stopping the rapid movement than correcting for errors (Liu & Todorov, 2007). Overall, the task-specific nature of the online adjustments fits well with the idea that visual signals about hand position are processed according to flexible, context-specific rules. Such flexibility of visual processing has been clearly demonstrated for motor planning (Sarlegna & Sainburg, 2007; Sober & Sabes, 2005) and the present study extends this view to the online control of goal-directed arm movements.

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