

Updating Target Location at the End of an Orienting Saccade Affects the Characteristics of Simple Point-to-Point Movements

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Six results are reported. (a) Reaching accuracy increases when visual capture of the target is allowed (e.g., target on vs. target off at saccade onset). (b) Whatever the visual condition, trajectories diverge only after peak acceleration, suggesting that accuracy is improved through feedback mechanisms. (c) Feedback corrections are smoothly implemented, causing the corrected and uncorrected velocity profiles to exhibit similar shapes. (d) Initial kinematics poorly predict final accuracy whatever the condition, indicating that target capture is not the only critical input for feedback control. (e) Hand and eye final variability are unrelated, suggesting that gaze direction is not a target signal for arm control. (f) Extent errors are corrected without modification of movement straightness; direction errors cause path curvature to increase. Together these data show that movements with straight paths and bell-shaped velocity profiles are not necessarily ballistic.

Keywords: feedback, reaching, eye–hand coordination, online control, forward model

Decades after the pioneering works of Woodworth (1899) and Bernstein (1967), the neural mechanisms involved in the generation of goal-directed actions are still, to a large extent, unknown. To address this issue, many authors have investigated simple point-to-point movements. On the basis of this paradigm, it has been repeatedly shown that reaching movements tend to exhibit straight line paths and roughly bell-shaped velocity profiles, irrespective of the initial and final locations of the hand (for a review, see Desmurget, Pélisson, Rossetti, & Prablanc, 1998). These typical features are often thought to reflect the central preplanning processes involved in reaching. The main aim of the present study is to investigate the validity of this common assumption.

Bell-Shaped Velocity Profiles Are Hallmarks of Ballistic Movements

In most point-to-point experiments, the basic paradigm is the same. The subject looks initially at a visual fixation point. His or her hand rests somewhere on the table. Suddenly, the fixation point is turned off, and a target diode is turned on in the peripheral visual field. When this happens, the subject has to look and point to the target as fast and accurately as possible. So that corrective feedback loops can be prevented from interacting with the original motor plan, the movements are often performed without visual feedback of the moving limb. In addition, the subjects are frequently required to point with a single uncorrected movement (Desmurget, Vindras, Grea, Viviani, & Grafton, 2000; Ghilardi, Gordon, & Ghez, 1995; Gordon, Ghilardi, & Ghez, 1994; Vindras & Viviani, 2002). This last point is quite interesting in that it emphasizes the widespread belief that online corrections cause the movement to exhibit jerky paths and irregular velocity profiles. Statements like the following are common in the literature:

Pointing movements were essentially ballistic. . . . The movement path was fairly straight. The velocity profile was single-peaked and showed no evidence of corrective submovements. (Vindras & Viviani, 2002, p. 284)

Single-peaked and approximately bell-shaped velocity profiles are considered as invariant characteristics of skilled preprogrammed movements. (Hermsdorfer et al., 1996, p. 1583)

The mean number of inversions in velocity (NIV) per stroke was used to quantify the mode of motor control during each PET scan.

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A NIV of 1 indicates fast open-loop processing. (Siebner et al., 2001, p. 726)

It has been well-documented that the underlying substructure of a movement can be inferred based on the location of the first zero crossings from negative to positive in the acceleration profile relative to the overall movement amplitude. This initial phase of the movement prior to the first acceleration zero crossing from negative to positive typically reflects the initial ballistic impulse toward the target, whereas the remaining portion of the movement reflects feedback-based correction. (Rand, Stelmach, & Bloedel, 2000, p. 209)

Although the quotes above are all fairly recent, the hypothesis that straight hand paths and bell-shaped velocity profiles are hallmarks of central planning processes has a long history. The main evidence supporting this view came from the idea that sensorimotor delays prevented feedback loops from affecting fast reaching movements (Hollerbach, 1982; Keele, 1968). To account for the fact that point-to-point movements were more accurate when vision of the hand was allowed (i.e., when feedback loops were exploitable), researchers suggested that responses requiring a high spatial precision were not uniform but segmented into two components: a ballistic component ensuring a fast transport of the hand to the vicinity of the target and a controlled component allowing fine spatial adjustments at the end of the trajectory (for reviews, see Desmurget & Grafton, 2003; Jeannerod, 1988; Meyer, Abrams, Kornblum, Wright, & Smith, 1988). The controlled component was supposed to rely on a direct comparison between the position of the target and the seen (vision) or felt (proprioception) location of the hand.

In the context of the model above, the feedback-related corrections were tracked by searching for jerky hand paths, asymmetric non-bell-shaped velocity profiles, and multiple acceleration zero crossings from negative to positive (Hermsdorfer et al., 1996; Meyer et al., 1988; Milner & Ijaz, 1990; Novak, Miller, & Houk, 2002; Rand et al., 2000). When the kinematic irregularities associated with the final phase of the movements were absent, as was the case in most classical reaching experiments, the characteristics of the motor responses were found to be remarkably compatible with the prediction of computational models involving purely feedforward control schemes. A robust match was observed, in particular, for the bell-shaped aspect of velocity profiles (Atkeson & Hollerbach, 1985; Flash & Hogan, 1985; Plamondon & Alimi, 1997), the curvature of movement paths (Desmurget & Prablanc, 1997; Flash, 1987; Harris & Wolpert, 1998; Uno, Kawato, & Suzuki, 1989), the pattern of end-point errors (Desmurget, Prablanc, Jordan, & Jeannerod, 1999; Flanders, Helms-Tillery, & Soechting, 1992; Gordon et al., 1994; Vindras, Desmurget, Prablanc, & Viviani, 1998), the final posture of the limb (Desmurget & Prablanc, 1997; Elsinger & Rosenbaum, 2003; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Englebrecht, 1995; Soechting, Bueno, Herrmann, & Flanders, 1995), and the amplitude of the movement (Desmurget, Grafton, Vindras, Grea, & Turner, 2003; Vindras & Viviani, 2002).

Eye-Hand Coordination: Target Location Is Reestimated After Hand Movement Onset

In spite of the evidence above, several observations make it difficult to believe that typical point-to-point movements are determined solely by central planning processes. The main ground

for suspicion comes from behavioral studies that have investigated the temporal organization of the eye-arm reaching system. When a subject is required to look and point as fast and accurately as possible to a target presented in his or her peripheral visual field, as is the case in most point-to-point experiments (see above), the overt response appears sequential: the eyes move 70–120 ms before the hand (Desmurget et al., 2001, 2004; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Prablanc, Pélisson, & Goodale, 1986; Sarlegna et al., 2003). Eye movement duration is typically within this range (Becker, 1989). This means that the hand usually starts moving before or just after completion of the primary saccadic response (Desmurget et al., 2001, 2004; Prablanc et al., 1979, 1986; Prablanc & Martin, 1992; Sarlegna et al., 2003).

A major implication of the observation above is that arm movement is planned before proper foveation of the target or, in other words, that the motor command initially sent to the upper limb is based on an estimation of the target location by the peripheral retina. This conclusion becomes all the more evident when electromyographic activity is considered. In this case, the motor response is recorded at the same instant for the eyes and the hand (Biguer, Jeannerod, & Prablanc, 1982; Gribble, Everling, Ford, & Mattar, 2002). The hand starts moving later because it has a greater inertia (for the biceps, for instance, the delay between the muscle contraction and the actual onset of the movement is typically within the range of 100–150 ms; Biguer et al., 1982; Godaux, Koulischer, & Jacquy, 1992; Turner, Owens, & Anderson, 1995). As reported in several studies, the peripheral retina does not allow a very accurate estimation of the target location (Bock, 1993; Prablanc et al., 1979). This implies that the initial motor plan sent to the arm should, at least, contain an error related to the crude estimation of the target location by the peripheral retina. At the end of the ocular saccade, that is, after hand movement onset, the target location can be recomputed on the basis of foveal or perifoveal information. It has been suggested that the updated visual signal is used by the nervous system to adjust the ongoing hand trajectory (Desmurget & Grafton, 2000, 2003; Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992; Prablanc et al., 1986). This suggestion implies that the kinematic characteristics of simple, visually directed, point-to-point movements are influenced by feedback mechanisms or, in other words, that reaching movements exhibiting straight paths and bell-shaped velocity profiles are not necessarily ballistic.

Amending Hand Trajectory When the Target Location Is Reestimated: The Double-Step Paradigm

From a conceptual point of view, the conclusions above are hard to reconcile with the idea that feedback loops rely exclusively on sensory information and in particular on vision of the effector during the movement. However, recent observations have demonstrated that the sensory models of feedback corrections are erroneous (for reviews, see Desmurget & Grafton, 2000, 2003). During the last decade, computational and behavioral studies have established that online feedback loops do, in fact, rely on a forward model that integrates the sensory inflow and motor outflow to evaluate the consequence of the motor commands sent to the arm. With such a model, the probable position and velocity of the effector can be estimated with negligible delays, and even predicted in advance, thus making feedback strategies possible for fast

reaching movements (Bhushan & Shadmehr, 1999; Gerdes & Happee, 1994; Miall & Wolpert, 1996; Todorov & Jordan, 2002). This point has been clearly demonstrated by Prablanc and colleagues in a series of studies involving a paradigm known as the “subliminal double-step” paradigm (Desmurget et al., 2001, 2004; Goodale et al., 1986; Péllisson et al., 1986; Prablanc & Martin, 1992). In this case, subjects are required to look and point to visual targets displayed in the peripheral visual field. During saccadic gaze displacement (when vision is suppressed), the target location is slightly modified. This modification triggers a change in hand trajectory, which deviates early from its initial path to reach the new target location. These deviations are generally not accompanied by detectable submovements. Also, they occur even when vision of the moving limb is not allowed, suggesting that nonvisual feedback loops (i.e., feedback loops that do not involve vision of the moving limb) represent the key mechanism for early hand trajectory control.

Several lines of evidence have even suggested that efferent motor output is the primary signal used to correct the ongoing movement in the context of double-step experiments. For instance, Bard et al. (1999) demonstrated that a deafferented patient was able to correct her movement online and to reach to a subliminally displaced target location despite the absence of visual or proprioceptive inputs. In agreement with this conclusion, behavioral studies have shown that the ongoing trajectory could be amended, in the dark, with a shorter latency than the minimal latency required to process proprioceptive information (Higgins & Angel, 1970). Also, it was demonstrated that altering the proprioceptive signals through tendon vibration did not modify the time required to respond to a visual perturbation (Jaeger, Agarwal, & Gottlieb, 1979).

Experimental Rationale: Determining the Influence of Target Foveation on Movement Characteristics

If the speculations above are true and if feedback mechanisms influence the ongoing arm trajectory after completion of the eye saccadic shift, how can we explain the remarkable ability of feedforward models to capture the main characteristics of simple, visually directed, point-to-point movements? A first hypothesis is that models of feedforward planning are so flexible that they can easily account for most aspects of motor performance, even aspects that are controlled in the real world by feedback mechanisms (Desmurget, Prablanc, & Rossetti, 1997). A provocative formulation of this idea was expressed by Morasso and Sanguineti (1997), who emphasized that “paradoxically, if a model fits the data too well it is a case of suspicion” (p. 548). A second alternative possibility might be that biases in the estimation of the target location by the peripheral retina are very small. In this case, the effective contribution of feedback loops to the characteristics of normal unperturbed movements would be marginal, if not null. One way to decide between these two possibilities is to contrast experimental conditions that are identical with respect to the planning phase but different with respect to the execution phase. For instance, the canonical reaching condition described in the first paragraph of the present introduction (*canonical*) can be compared with a condition in which the target location is turned off after eye movement onset, around the peak velocity of the saccadic response (*off*). Because arm movement starts before completion of the saccadic response (see above), the motor program underlying the

initial arm responses in the two conditions should be identical. However, in the second condition, when the target disappears during the saccadic shift, there is no possibility for the motor system to reevaluate the location of the target at the end of the ocular movement. If there are no differences between the canonical and off conditions, then one would conclude that the initial errors related to an erroneous estimation of the target location by the peripheral retina are either small or uncorrected during the movement.

A possibility that is not addressed by the two conditions above is that the saccadic signal itself, or the ability to anchor the eye at the vicinity of the target, provides critical information to guide the hand and update the initial motor plan (Enright, 1995; Flanders, Daghestani, & Berthoz, 1999; Soechting, Engel, & Flanders, 2001). To address this possibility, one could contrast the first two conditions with a third condition in which (a) the target is turned off at hand movement onset and (b) saccadic activity is not permitted (the eyes remain anchored at the fixation point; *fixation*). If eye and hand movements are really planned in parallel, the early characteristics of the movements should be the same in the three experimental conditions. In addition, if feedback loops really affect the movement in the canonical or the off conditions, spatial and kinematic differences should appear during the course of the movement between these conditions and the fixation condition.

Experimental Rationale: Contrasting Early and Late Kinematic Markers to Determine the Contribution of Central Planning Processes

In addition to comparing different experimental conditions, a potentially powerful way to determine the degree to which a movement is preprogrammed is to correlate the early kinematic markers of the trajectory (e.g., initial acceleration) with the final characteristics of the movement. This technique was first developed by Gordon and coworkers in the context of isometric movements (Gordon & Ghez, 1987a, 1987b). It was shown that the initial peaks of the first and second time derivatives of force were strongly predictive of the peak force achieved and were correlated with the target force. This was taken as an indication that “response trajectories must have been largely preprogrammed, and, further, [that] the degree to which the initial peak d^2F/dt^2 predicts the peak force achieved represents a measure of the contribution of a preplanned motor program to trajectory formation” (Gordon & Ghez, 1987a, p. 241).

The pioneering approach used by Gordon et al. to assess the degree of preprogramming of the trajectory was subsequently used in several studies dealing with point-to-point movements (Fisher, Winstein, & Velicki, 2000; Messier & Kalaska, 1999). Only modest correlations were reported in these studies. For reaching movements directed at predictable and unpredictable targets, Fisher et al. (2000) reported that the percentage of final variance in movement amplitude that could be explained by the initial variance in movement peak velocity ranged from 37% (predictable targets) to 45% (unpredictable targets). On the basis of this result, the authors concluded that “it does not appear that the ‘planned’ component was governed by a pulse-height control strategy” (Fisher et al., 2000, p. 340). A potential problem with this study is that peak velocity is not always a reliable correlate of movement preplanning. Indeed, several studies have shown that peak velocity can be influenced strongly by online feedback loops (Desmurget et al.,

2004; Prablanc & Martin, 1992). This uncertainty was not present in the study carried out by Messier and Kalaska (1999). These authors reported, for reaching movements directed at memorized targets, that only 16% of the final variance in movement amplitude could be explained by the initial variance in movement peak acceleration (36% when peak velocity was considered). On the basis of these results, Messier and Kalaska concluded that “end-point distributions are not completely predetermined by the initial kinematics” (Messier & Kalaska, 1999, p. 139).

The work of Messier and Kalaska (1999) raises two questions. First, would higher correlations be observed between peak acceleration and movement amplitude for movements directed at actual (nonmemorized) targets, as could be expected from the pioneering study of Gordon and Ghez (1987a)? Second, would a richer correlation model disclose higher correlation levels? With respect to this point, it has been shown, for instance, that the amplitude of the movement does not depend only on the maximal magnitude of the hand acceleration (or velocity). Movement amplitude is also influenced by the time required to reach the peak acceleration (Gordon & Ghez 1987b; Jeannerod, 1988; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). As a consequence, multiple correlation models involving both the peak and time to peak acceleration might reveal consistently better correlations than do simple models involving only the peak hand acceleration. This possibility was tested in the present experiments. We reasoned that correlations between a movement’s initial kinematics and its end-point measures should be consistently high when no updating of the target location is allowed at the end of the saccadic shift. By contrast, we predicted that correlations should be modest when this updating is allowed.

Summary

When subjects point to visual targets presented in the peripheral visual field, the arm starts moving before target foveation. The manual response is thus planned to reach a location estimated through the use of the peripheral visual system. This location is thought to be imprecise. In light of these premises, we address four questions in the present study: (a) Can we find convincing evidence that the initial errors related to an erroneous estimation of the target location by the peripheral visual system are corrected during the movement? (b) If yes, do the corrections generate zero crossings in the acceleration profile or are they smoothly integrated to the ongoing trajectory? (c) In this case, is it possible to find reliable markers allowing distinction between the corrected and uncorrected movements (e.g., path curvature, lengthened deceleration, modulation of the peak velocity)? (d) How robustly can we predict the final variance in movement accuracy on the basis of the initial variance in movement acceleration when the information available for feedback control is minimized (no saccade, target off at hand movement onset)? Answers to these questions will both elucidate the nature of simple point-to-point movements and cast further doubt on the common misperception that reaching movements presenting with roughly straight paths and single-peaked, bell-shaped velocity profiles are determined solely by feedforward planning processes.

Experiment 1: Modulating Movement Amplitude

In this first experiment, we studied movements performed along a frontoparallel line for both the eyes and the hand. We mainly

manipulated two factors: (a) the ability of the subject to perform a saccade and (b) the ability of the subject to see the target at the end of the saccade and/or during the movement. Vision of the moving limb was never allowed.

Method

Subjects

Six subjects (3 men and 3 women, ages 29–49 years) participated in this experiment, after their informed consent was obtained. They were all free of neurological deficits, right-handed, and naive about the purpose of the study. The experimental procedure was approved by the Human Investigations Committee of Emory University.

Apparatus

A schematic representation of the experimental apparatus used in the present study is presented in Figure 1. This apparatus is similar to one used in previous experiments (Desmurget et al., 2000, 2003). In brief, it consisted of a horizontal digitizing tablet to record the planar movements of a handheld mouse (250 Hz sampling rate, ± 0.05 mm resolution). The digitizing tablet was designed to minimize frictional forces. Antifriction cushions were also placed under the handheld mouse with the same purpose. The height of the table was adjusted such that the height of the chin rest supporting the head of the subject was 29 cm above the table. In this configuration, the table was roughly level with the lower part of the subject’s sternum, and the eyes were 40 cm above the pointing surface. An array of red LEDs and a half-reflecting mirror were suspended over the pointing surface. Looking down at the mirror, the subject saw the virtual image of the LEDs in the plane of the pointing surface. With this device, the reaching hand could not occlude the virtual image of the LEDs, which prevented the subject from gaining an indirect feedback of his or her reaching accuracy. A light source was placed between the pointing table and the mirror. When turned on, it allowed the subject to see his or her hand. The hand starting position (S) was located 30 cm in front of the subject’s head. Four red targets were used. They were located along a frontoparallel line (i.e., parallel to the subjects’ shoulders) at 60 mm (T1), 120 mm (T2), 180 mm (T3), and 240 mm (T4). A green target indicated the hand starting location (0 mm). The subjects had to point using a handheld mouse identical to the one described in an earlier study (Desmurget, Jordan, Prablanc, & Jeannerod, 1997). They were explicitly instructed to maintain the handheld mouse on the table during the whole movement. All movements that did not satisfy this criterion were cancelled and presented again later in the session. When the hand was at the starting point, the forearm rested on the table in a semiflexed position. Neither the arm nor the forearm were actively supported or maintained during the movement.

Experimental Conditions and Procedure

The subjects were instructed to “point as accurately as possible with a single uncorrected movement” (the subjects were told that they should cover the target with their index fingertip). They were asked not to generate additional movements at the end of the trial, even when they felt their pointing was not totally accurate. No special emphasis was put on velocity or on movement duration. At the beginning of the study, the subjects were trained until they felt comfortable with both the task and the apparatus. The training session never took more than 15 trials. Five experimental conditions were tested.

Saccade permitted, with target on until end of hand movement (S-endH). The subjects were free to move their eyes, and the target remained on during the whole trial. In this case, updating of the target location was allowed at the end of the gaze shift, and the presence of the target could potentially be used to guide the hand during the ongoing trial.

Saccade permitted, with target on until end of eye movement (S-endE). The subjects were free to move their eyes, and the target was turned off 50 ms after the end of the ocular saccade. This condition allowed updating of

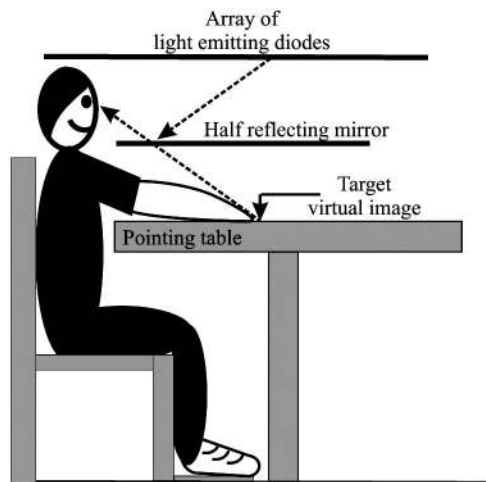
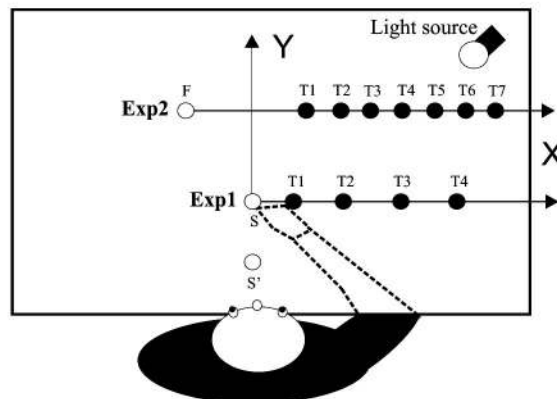


Figure 1. Schematic representation of the experimental apparatus for the first (Exp1) and second (Exp2) experiments. F = gaze fixation target; T = target; S and S' = hand starting positions for Exp1 and Exp2, respectively.



the target location at the end of the gaze shift but prevented the use of ongoing vision of the target to guide hand movement.

Saccade permitted, with target on until beginning of eye movement (S-begE). The subjects were free to move their eyes, and the target was turned off 20 ms after onset of the ocular saccade. This condition prevented both updating of the target location at the end of the saccadic response and the use of ongoing vision of the target to guide hand movement.

Fixation required, with target on until beginning of hand movement (F-begH). The subjects had to look at a fixation point positioned on the hand starting position while pointing to a target presented in the peripheral visual field. The target was turned off at hand movement onset. The fixation point remained on during the whole trial. In this case, the subject could not use the saccadic signal, the updating of the target location at the end of the saccadic response, or the actual presence of the target during the movement to amend the ongoing response.

Fixation required, with target on until end of hand movement (F-endH). The subjects had to look at a fixation point positioned on the hand starting position while pointing to a target presented in the peripheral visual field. The target and the fixation point remained on during the whole trial. In this case, the subject could not use the saccadic signal or the updating of the target location at the end of the saccadic response to amend the ongoing response. The target was visible during the movement for potential motor corrections.

Each trial involved 6 steps. (a) The green target (starting point) and the light allowing vision of the arm at rest were turned on. (b) The subject placed his or her index fingertip at the starting location using direct visual feedback (a small adhesive sticker was placed on the nail of the subject to ensure accurate positioning). (c) The light illuminating the subject's hand was turned off, followed by a delay varying randomly between 1 and 1.5 s. During this time the subject was required to look at the green diode located on the hand starting location. (d) A red target was turned on in the peripheral visual field, triggering the reaching response of the subject. (e) At the end of the trial, the subject was required to move his or her hand in front of him or her as close as possible to the edge of the table. This step was included to prevent the subject from comparing the actual hand position with the position where he or she thought the hand was. (f) The illuminating light was turned on again. When a saccade was detected in the fixation conditions, the trial was canceled and represented later in the session.

The five conditions were presented in separate blocks. These blocks were randomly ordered across subjects. In each block, each subject per-

formed 40 trials (4 targets \times 10 repetitions). Within each block, the different target locations were randomly intermixed.

Movement Recording and Data Analysis

During the experiment, eye position signals were collected at 500 Hz with binocular direct current electrooculography (EOG). Eye velocity was extracted online from the position signal with a two-point central difference derivative algorithm (Bahill & McDonald, 1983). Prior to the experiment, the subjects were required to perform a series of saccades from the fixation point toward the different targets. This procedure allowed determination of the noise inherent to the recording system and determination of a threshold for saccadic onset and saccadic ending. In S-begE, the target was turned off 20 ms after the estimated saccadic onset (i.e., 20 ms after eye velocity passed above threshold). In S-endE, the target was turned off 50 ms after the estimated saccadic ending (i.e., 50 ms after eye velocity passed below threshold).

The calibration of the EOG signal was performed in two steps. First, the eccentricity of the different targets was computed in polar coordinates with respect to the cyclopean eye. When expressed in eye-centered coordinates, the target eccentricities were 0° (hand starting point), 6.8° (T1), 13.5° (T2), 19.8° (T3), and 25.6° (T4). Note that these values were estimated assuming that the chin-eye distance was equal to 11 cm (the slight errors that could result from this estimation are constant for a given subject, and they are thus unable to explain systematic differences between the experimental conditions). Second, the EOG signal was measured while the subject looked at the different targets. A calibration curve was then computed from these measurements by fitting a polynomial through the data. This curve was used to transform the EOG signal into a calibrated eye position signal. Before calibration, the tendency of the EOG signal to drift over time was corrected by zeroing, for each trial, the raw signal recorded during the first 50 ms of the fixation period (Pélisson, Prablanc, & Urquizar, 1988). Consistency of the gain of the EOG signal was also checked by comparing the raw gain (in volts) of the saccadic displacement for each target across the different sessions (1–5). No difference was found. Once calibrated, the eye position signal was numerically filtered at 30 Hz with a zero-phase, finite-impulse response filter. The velocity signal was computed, from the filtered position signal, with a two-point central difference derivative algorithm (Bahill & McDonald, 1983). The onset and the end of the primary saccade were automatically detected through the use of a velocity threshold procedure ($20^\circ/s$). The main saccadic characteristics analyzed in

this experiment were the eye reaction time (RT_{eye}), the duration of the primary saccadic response (MD_{eye}), the magnitude of the primary saccadic response, and the final eye position. The final eye position was defined as the eye position reached at the end of the trial.

For hand movements, the position signals delivered by the digitizing tablet were expressed in an orthogonal frame of reference (see Figure 1). This frame was centered on the hand starting point. The y -axis was sagittal and oriented forward; the x -axis was frontoparallel and oriented rightward. The x and y position signals delivered by the digitizing tablet were filtered at 15 Hz with a zero-phase, finite-impulse response filter. Movement velocity was computed from the filtered position signal with a two-point central difference derivative algorithm (Bahill & McDonald, 1983). The same method was used to compute hand acceleration from the velocity signal. The onset and the end of the hand movement were determined automatically through the use of the following threshold: hand velocity = 30 mm/s and hand acceleration = 500 mm/s². (These values were chosen to statistically fit with the values obtained from a visual inspection of the data.) Movement onset and movement end were used to compute the movement duration (MD) and the movement reaction time (RT). In addition to these variables, the following indicators were also used to characterize the performance of the subjects.

Accuracy indicators for movement end point. The movement final error was decomposed into systematic and variable errors. The systematic error was expressed in polar coordinates as amplitude and direction errors. Amplitude error was defined as the difference between the actual movement amplitude and the required movement amplitude. Likewise, direction error was defined as the angular difference between the actual movement direction and the required movement direction. The variable end-point error was defined as the 95% confidence ellipse of the end-point distribution (Johnson & Wichern, 1982). Three main variables were used to characterize the detailed characteristics of end-point error confidence ellipses: (a) the area; (b) the shape (ratio of the lengths of the axes of the confidence ellipses, i.e., major axis/minor axis); and (c) the orientation (angle between the major axis of the ellipse and the mean movement direction).

Accuracy indicators for movement path. Hand path variability was computed through the use of a procedure described by Goodbody and Wolpert (1998; see also Desmurget et al., 2004). In brief, the hand position, for each movement, was resampled at 50 evenly spaced points along the path length. For each point of the resampled trajectory, a 95% confidence ellipse was computed. The variables used to characterize the confidence ellipses computed for each point along the trajectory were the same as the ones described for the end-point confidence ellipses.

Kinematic indicators. The main kinematic landmarks were computed, namely peak and time to peak acceleration, peak and time to peak velocity, and peak and time to peak deceleration.

Submovement indicators. Each individual response was examined to check for the presence of corrective submovements during the deceleration phase (i.e., from peak velocity to the end of the movement). Submovements were detected as zero crossings of the acceleration profile (Elliott, Carson, Goodman, & Chua, 1991; Rand et al., 2000; Turner, Desmurget, Grethe, Crutcher, & Grafton, 2003). To avoid spurious detections, we required that a change in sign of the acceleration value had to last for more than 20 ms to be considered as reflective of the occurrence of a submovement.

Shape indicators for hand path. To determine whether movement path presented a similar shape across the different experimental conditions, we extended a method initially developed by Atkeson and Hollerbach (1985). For each movement, the line (L) connecting the start and end positions was computed. Seven equidistant points were then defined along this line (i.e., 12.5%, 25%, 37.5%, 50%, 62.5%, 75%, 87.5% of the length of L). For each of these points, the distance d of the actual path to L was determined and normalized for movement amplitude (d was divided by the length of L). D is the variable that resulted from these computations. We reasoned that if two trajectories present the same shape, then for all the points selected on

L , D should be identical. By contrast, if two trajectories are different, D should be different for at least one of the selected points. Using a similar procedure, we also determined the maximal deviation from the actual hand path to L . This variable represents the maximal movement curvature. It is probably the most common variable used in the literature to characterize hand path shapes (Atkeson & Hollerbach, 1985; Desmurget et al., 1999; Gordon et al., 1994).

Shape indicators for hand velocity. The symmetry and global shape of each velocity profile were estimated. The symmetry was determined by computing the relative time to peak velocity (peak velocity/MD). Perfectly symmetric profiles have a symmetry value of .5. When the acceleration phase is shorter than the deceleration phase, the symmetry value is smaller than .5. When the acceleration phase is longer than the deceleration phase, the symmetry value is higher than .5. The global shape of the velocity profiles was estimated by dividing the peak velocity by the average velocity of the movement. If two profiles have the same shape, this ratio is constant (Novak, Miller, & Houk, 2000; Soechting, 1984).

Beyond these common synthetic indicators, more sensitive approaches have been developed in the literature to estimate the shape of the velocity profiles. Among these approaches, the one proposed by Atkeson and Hollerbach is probably the most common (Atkeson & Hollerbach, 1985). It has been implemented here. The main idea is as follows: Each profile is first normalized for distance and duration and then compared with a reference profile arbitrarily chosen. In the present experiment, the reference profile was an individual profile performed by 1 subject. This profile was selected because it was devoid of corrective submovement and because its symmetry index was close to .5. The differences between the reference and actual profiles is then evaluated through the use of a similarity index. Significant variations in the shape of two profiles (e.g., symmetry, number of submovements) cause significant variations of the similarity index. Computationally, normalization of the velocity profiles for distance and duration involves the following transformation (see Atkeson & Hollerbach, 1985, for details): $V_{norm} = cV_{exp}(c/at)$, where t is the time scale and c is the scaling factor for duration. This factor is equal to the ratio of the maximal velocity of the reference profile (V_{ref}) to the maximal velocity of the experimental profile (V_{exp}). The maximal velocity was used rather than the movement duration because of imprecision in determining movement start and stop. The variable a is the scaling factor for distance. This factor is equal to the ratio of the distance of the reference profile (d_{ref}) to the distance of the experimental profile (d_{exp}). The index of similarity is determined with the following formula: $w = (A \cup B - A \cap B)/B$, where A and B are the areas under the experimental and reference curves, respectively. In this case, $A \cup B$ is the total area contained beneath both curves, whereas $A \cap B$ is area common to both curves. If the curves are strictly identical, w is null. For each individual trial, the alignment of the experimental profile with the reference profile was selected to minimize w .

A two-way analysis of variance (ANOVA) with repeated measures was used to identify significant differences in kinematic markers between the experimental conditions. The repeated measures factors were condition (five levels for hand-related variables: S-endH, S-endE, S-begE, F-endH, F-begH; three levels for eye-related variables: S-endH, S-endE, S-begE), and target location (four levels: T1, T2, T3, T4). Duncan's multiple-range test was used for post hoc comparisons of the means (Winer, 1971). The threshold for statistical significance was set at .05.

In addition to investigating the existence of significant differences between the experimental conditions, we also conducted specific analyses to address the hypothesis that gaze location represents an attractor to which the hand is directed (see the introduction). If such is the case, one may expect the hand movement to be more accurate in S-begE (the gaze is anchored at the vicinity of the target) than in F-begH (the gaze remains located at the starting point). Also, one may predict that the final positions reached by the eye and the hand will vary concurrently. In light of earlier studies (Prablanc et al., 1979, 1986), one may expect the variability in gaze final location to be greater in S-begE than in S-endE and S-endH. On this basis, one may predict that if the gaze location really plays the role of an

attractor for the hand, then the variability in hand amplitude should follow the same trend, that is, be larger in S-begE than in the two other conditions. To quantitatively address this hypothesis, we computed for each subject, each condition, and each target ($n = 10$ trials) the ratio of the eye amplitude standard deviation to the hand amplitude standard deviation. Another, complementary approach would be to determine linear coefficient of correlation between the hand and eye movement amplitudes (Prablanc et al., 1979). We rejected this approach on the ground that an EOG signal is not accurate enough to allow the correlations between hand and eye final locations to be reliably computed (Prablanc et al., 1979).

The last set of analyses conducted in this study concerns the degree of preprogramming of the movement. If reaching movements are determined by feedforward central planning processes, it should be possible to predict end-point accuracy reliably on the basis of the early characteristics of the movement (Fisher et al., 2000; Gordon & Ghez, 1987a, 1987b; Messier & Kalaska, 1999). To study this possibility, we first investigated whether movement amplitude could be predicted on the basis of the characteristics of the acceleration phase. Two parameters were used to characterize the acceleration phase: the peak and the duration of the movement acceleration. For each subject, each condition, and each target eccentricity, we determined the multiple correlation coefficient (R) with movement amplitude as the independent variable and peak acceleration and time to peak velocity (duration of the acceleration phase) as the dependent variables. A potential concern with this approach is that feedback loops can influence the ongoing movement before peak velocity (Desmurget et al., 2004; Prablanc & Martin, 1992). As a consequence, it is not clear whether the duration of the acceleration phase is really reflective of movement planning or whether it is also influenced by feedback loops (see van der Meulen, Gooskens, Denier van der Gon, Gielen, & Wilhelm, 1990). A second analysis was thus conducted based on two kinematic parameters that are truly thought to reflect movement planning: the peak and time to peak acceleration. The multiple correlation coefficient was then determined with movement amplitude as the independent variable and peak acceleration and time to peak acceleration as the dependent variables. In this analysis and the previous one, the coefficient was computed after subtraction of the partial correlations between the dependent variables (Maxwell & Delaney, 1990).

Results

For the sake of simplicity, the S-endH and S-endE conditions are sometimes named *updating* conditions in the following text. The three other conditions are called, by contrast, *no updating* conditions.

Eye-Hand Coordination: Arm Motor Command Is Issued Prior to Saccade Completion

On average, RT_{eye} was equal to 209 ms. This variable was not affected by the condition factor, $F(2, 10) = 1.0, p > .35$, but it was found to vary significantly as a function of the target factor, $F(3, 15) = 5.8, p < .01$. RT_{eye} decreased with the magnitude of the saccadic shift (T1: 218 ms; T2: 211 ms; T3: 208 ms; T4: 199 ms). No interaction was observed between the experimental factors for RT_{eye} , $F(6, 30) = 0.3, p > .90$. The same pattern of variation was observed for MD_{eye} . On average, MD_{eye} was equal to 72 ms. The duration of the saccadic displacement was not affected by the condition factor, $F(2, 10) = 1.2, p > .30$, but it was found to increase monotonically as a function of the target eccentricity, $F(3, 15) = 203.1, p < .0001$ (T1: 45 ms; T2: 69 ms; T3: 83 ms; T4: 93 ms). No interaction was observed between the experimental factors for MD_{eye} , $F(6, 30) = 1.7, p > .15$.

On average, RT_{hand} was equal to 330 ms. This variable did not depend on the experimental condition, $F(4, 20) = 1.0, p > .40$, but

was significantly affected by the eccentricity factor, $F(3, 15) = 10.0, p < .001$. No interaction was observed for RT_{hand} , $F(12, 60) = 0.5, p > .90$. The significant main effect of the eccentricity factor reflected the existence of a slight decrease of RT_{hand} with the movement amplitude (T1: 340 ms; T2: 332 ms; T3: 325 ms; T4: 323 ms). Like RT_{hand} , MD_{hand} varied with the eccentricity factor, $F(3, 15) = 69.0, p < .0001$, but not with the condition factor, $F(4, 20) = 0.8, p > .50$. No interaction was observed for MD_{hand} , $F(12, 60) = 0.5, p > .90$. On average, MD_{hand} was equal to 721 ms. It increased monotonically as a function of the movement magnitude. MD_{hand} was equal to 548, 699, 774, and 864 ms for the T1, T2, T3, and T4 targets, respectively.

The previous results indicate that hand movement onset occurred, for all conditions, a few tens of milliseconds after the end of the saccade. The delay between the beginning of the hand movement and the end of the saccadic response ($RT_{hand} - [RT_{eye} + MD_{eye}]$) decreased with the target eccentricity, due to the fact that MD_{eye} increased with the movement amplitude. This delay ranged from 77 ms for the T1 target to 31 ms for the T4 target. As is emphasized in the discussion, these values are too small to support the idea that arm movements were planned and initiated after completion of the primary saccadic response, that is, after updating of the estimation of the target location by foveal vision. No reaction time can be that fast, especially if one considers the existence of consistent delays between the actual muscle contraction and the onset of the movement (100 to 150 ms; Biguer et al., 1982; Godaux et al., 1992; Turner et al., 1995).

Eye Movement Accuracy: A Corrective Saccade Allows Proper Target Foveation in the Updating Conditions

In the S-endH and S-endE conditions, a vast majority of responses (>90%) consisted of two phases, as expected from earlier studies (Deubel, Wolf, & Hauske, 1982; Harris, 1995; Prablanc & Jeannerod, 1975): an initial saccade undershooting the target position and covering on average 92.1% of the required displacement and a corrective saccade having a mean latency of 165 ms with respect to the completion of the first saccade and achieving accurate target foveation. Corrective saccades were present in only a minority of trials in the S-begE condition (<10%), as reported in previous studies (Prablanc & Jeannerod, 1975; Prablanc et al., 1986; but see Becker, 1976). For S-begE, the magnitude of the primary saccadic response (90.0%) was not statistically different from the magnitude of the final gaze location (89.9%).

The difference in final gaze eccentricity between S-begE and the two other conditions was confirmed by the existence of a significant effect of the condition factor on the final eye location: $F(2, 10) = 352.0, p < .0001$. As indicated by post hoc analyses, S-begE was significantly different from S-endH and S-endE ($p < .0005$). The difference observed between the latter conditions was not significant ($p > .30$). These results are illustrated in Figure 2, which displays, for 1 subject, representative saccadic responses toward all targets in all conditions.

Of interest, a significant Target \times Condition interaction was observed for the final eye location, $F(6, 30) = 57.4, p < .0001$. This interaction can be explained as follows: (a) for S-endH and S-endE, the final eye location was always located on the target after completion of the corrective saccade; (b) for S-begE, an eccentricity-related effect was observed due to the absence of corrective saccades in most cases. (Because the saccadic response

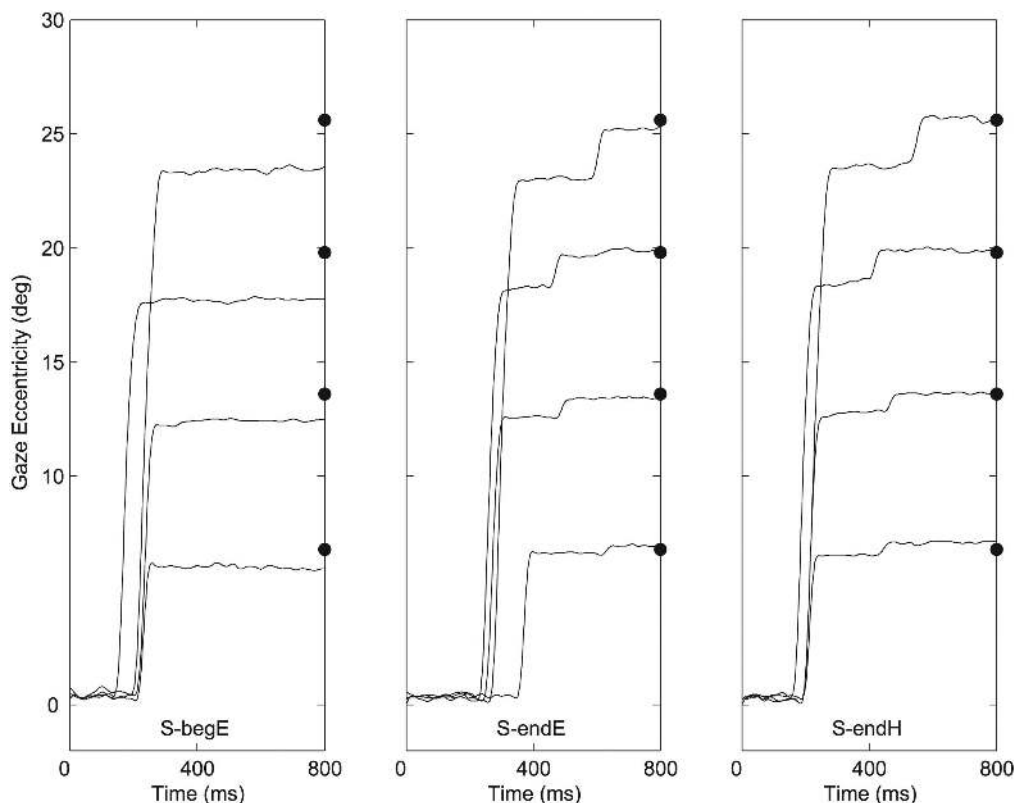


Figure 2. Representative saccades performed by 1 subject in the three experimental conditions toward each target (black circles represent the target eccentricity). In the S-endH and S-endE conditions, the saccadic response involves an initial saccade undershooting the initial target position and a corrective saccade achieving accurate target foveation. This corrective saccade is not present in the S-begE condition. In this case, the gaze eccentricity undershoots the target eccentricity. deg = degrees; S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement.

represented around 90% of the required displacement, the eye undershoot increased with the target eccentricity.) This eccentricity-related effect can be observed in Figure 2 (left panel).

Hand Accuracy: Extent Errors Are Reduced in the Updating Conditions

A clear effect of the condition factor on the movement accuracy was observed. This effect concerned mainly the movement amplitude. As can be seen in Figure 3, movement amplitude was significantly affected by both the experimental task, $F(4, 20) = 6.6, p < .002$, and the target eccentricity, $F(3, 15) = 34.9, p < .0001$. The significant effect of the target factor on amplitude error was related to the presence of an eccentricity-related effect. Although the hand motor response was, on average, hypometric for all target locations, the degree of hypometria increased with the movement magnitude (T1: -2.6 mm; T2: -13.7 mm; T3: -35.0 mm; T4: -44.6 mm; see Figure 3). This eccentricity-related effect was present for all experimental conditions, explaining the absence of a Condition \times Target interaction, $F(12, 60) = 1.1, p > .40$. The significant effect of the condition factor on amplitude errors indicated that movement extent was affected by the experimental condition. Post hoc analyses revealed three important points:

1. The anchoring of gaze in the vicinity of the target and/or the ability to move the eyes did not consistently improve movement accuracy. Although amplitude error was slightly smaller in S-begE (-28.0 mm) than in F-begH (-30.3 mm) and F-endH (-31.4 mm), the difference observed between these three conditions was not significant ($p > .45$).

2. The ability to update the estimation of target location at the end of the saccadic shift improved movement accuracy substantially. On average, amplitude error was 13 mm larger in S-begE (-28.0 mm) than in S-endH (-15.2 mm) and S-endE (-15.0 mm; $p < .02$). Although small at first glance, this 13 mm difference is far from negligible. It represents around 10% of the mean movement amplitude observed in the S-begE condition (i.e., movement amplitude was increased by 10% when the subject had the opportunity to update the target location at the end of the saccadic shift).

3. The ability to see the target during the course of the movement did not significantly improve end-point accuracy. Amplitude error was not different in F-endH/F-begH ($p > .75$) or in S-endE/S-endH ($p > .95$).

Regarding the direction error, a general counterclockwise shift was observed (12° on average). This shift was similar in all conditions, $F(4, 20) = 1.5, p > .20$. It decreased with the target

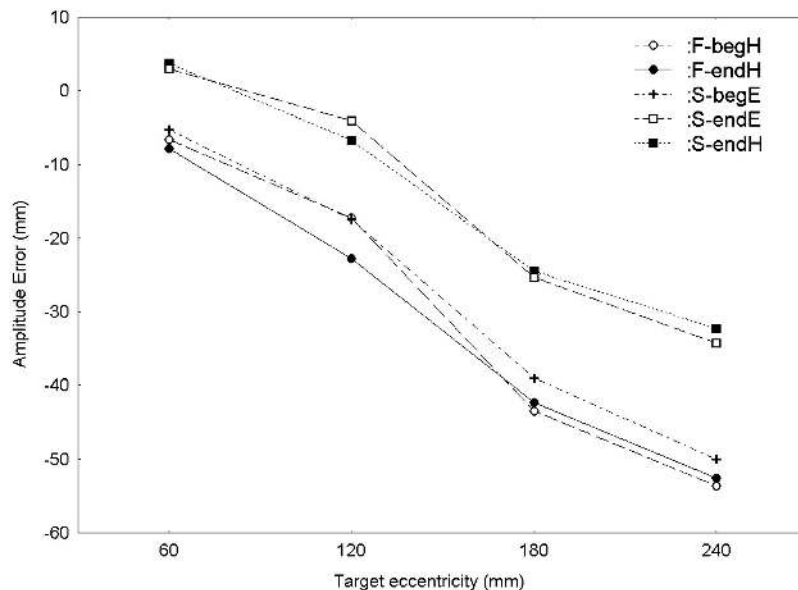


Figure 3. Variation of the mean amplitude error as a function of the experimental conditions. Note that the tendency to undershoot the target increases with the target eccentricity for all experimental conditions. Note also that the error in movement amplitude is smaller in S-endE and S-endH than in the three other experimental conditions. F-begH = fixation required, with target on until beginning of hand movement; F-endH = fixation required, with target on until end of hand movement; S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement.

distance, which accounts for the significant effect of the target factor on direction error, $F(3, 15) = 19.6, p < .0001$. No Condition \times Target interaction was observed for direction error, $F(12, 60) = 0.4, p > .90$.

Hand Accuracy: Directional Variability Decreases Progressively During the Second Half of the Movement in the Updating Conditions

In agreement with earlier studies (Desmurget, Jordan, et al., 1997; Gordon et al., 1994; Messier & Kalaska, 1997; Vindras & Viviani, 1998) and as illustrated in Figure 4, our data indicate that the movement end points tended to be clustered in an elliptical pattern oriented along the mean movement axis. The angle between the major axis of the end-point ellipse and the mean movement direction (-1.7° on average) did not change as a function of the target, $F(3, 15) = 0.5, p > .65$, condition, $F(4, 20) = 0.7, p > .60$, or interaction, $F(12, 60) = 1.2, p > .30$, factors. This remarkable stability was not observed for the shape of the confidence ellipse. Although this variable was not affected by the target, $F(3, 15) = 2.1, p > .10$, and interaction, $F(12, 60) = 1.7, p > .08$, factors, it was significantly influenced by the condition factor, $F(4, 20) = 8.2, p < .0005$. As shown by post hoc tests, the ratio of the major to the minor axis of the 95% confidence ellipse was significantly larger when updating of the target location was allowed after the saccadic shift (S-endE: 3.04 and S-endH: 3.21 vs. S-begE: 1.86, F-begH: 2.33, and F-endH: 1.98; $p < .005$). As indicated by further analyses, this variation of the shape of the movement-end-point scatter was mainly related to a decrease of the length of the minor axis of the confidence ellipse, that is, of the variability in movement direction, considering that the long axis of the ellipse

always approximated the mean movement direction (F-begH: 11.2 mm; F-endH: 12.5 mm; S-begE: 12.5 mm; S-endE: 7.0 mm; S-endH: 6.7 mm), $F(4, 20) = 6.9, p < .002$. The length of the long axis of the confidence ellipse (i.e., the variability in movement extent) was not significantly different across the experimental conditions (F-begH: 24.9 mm; F-endH: 23.0 mm; S-begE: 22.4 mm; S-endE: 19.3 mm; S-endH: 19.9 mm), $F(4, 20) = 1.6, p > .20$.

Our data also revealed a modification of the area of the end-point confidence ellipse as a function of condition, $F(4, 20) = 3.3, p < .04$, and target, $F(3, 15) = 24.7, p < .0001$, factors. As shown by post hoc analyses, the confidence area increased with the movement distance (T1: 319 mm²; T2: 631 mm²; T3: 910 mm²; T4: 1,227 mm²) and decreased with the ability to update target location at the end of the saccadic shift. With respect to this latter point, the confidence area was greater in the F-endH (1,005 mm²), F-begH (996 mm²), and S-begE (989 mm²) conditions than in the S-endE (457 mm²) and S-endH (453 mm²) conditions ($p < .004$). This effect is consistent with the decrease of the length of the minor axis of the end-point confidence ellipse in the two latter conditions (see above). There was no Target \times Condition interaction for the area of the end-point confidence ellipse, $F(12, 60) = 1.6, p > .10$.

In light of the results above, specific analyses were conducted to investigate whether the reduction in direction variance was really due to a feedback process or whether it was associated with modifications in movement planning. Theoretically, feedforward modifications could occur as a result of prior experience in the block: All movements are performed in the same direction, and every trial provides direction information that could be used to plan the next movement. If this hypothesis is true, the initial

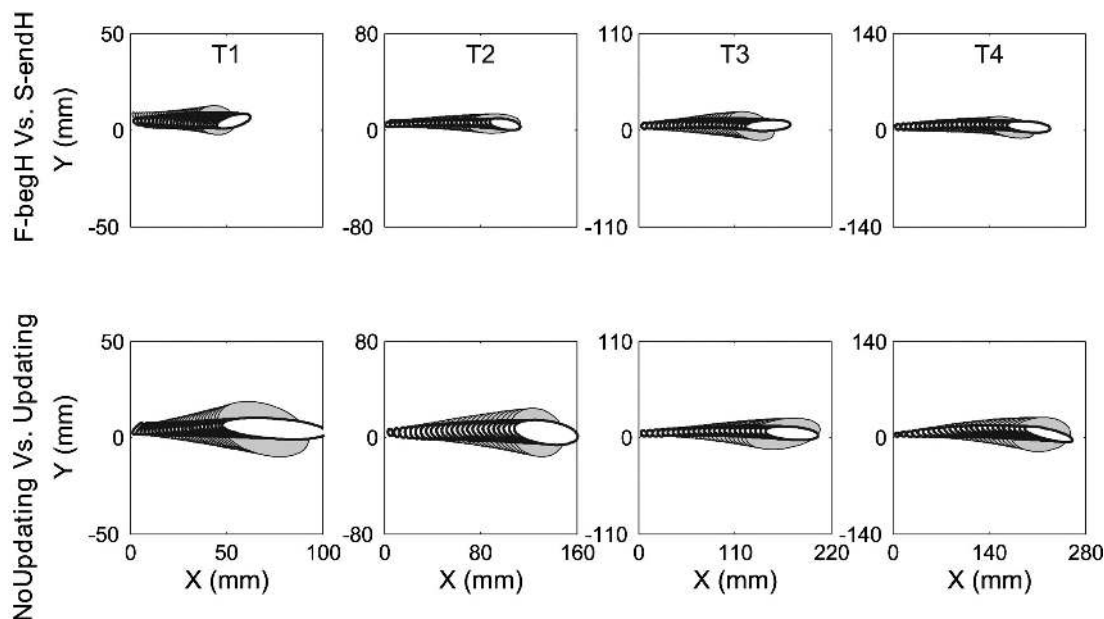


Figure 4. Spatial variability observed along the hand path for a single subject. These data were obtained by resampling hand position, for each individual movement, at 50 evenly spaced points along the path length (see the *Method* section of Experiment 1). The top row compares the two conditions that respectively minimize (F-begH) and maximize (S-endH) the amount of information available for feedback control. The bottom row merges the conditions allowing updating of the target location at the end of the saccadic shift (S-endH, S-endE) with the conditions that do not (F-begH, F-endH, S-begE). T = target; F-begH = fixation required, with target on until beginning of hand movement; S-endH = saccade permitted, with target on until end of hand movement; S-endE = saccade permitted, with target on until end of eye movement; F-endH = fixation required, with target on until end of hand movement; S-begE = saccade permitted, with target on until beginning of eye movement.

direction of the movement should be less variable in the conditions allowing updating of target location. By contrast, if the reduction in directional variance really occurs during the movement, comparable variability should be observed in all conditions at the beginning of the movement. The variability of the initial movement direction was defined for each subject, each condition, and each target by averaging the instantaneous movement direction over the first 40 ms of the movement. A two-way ANOVA (Condition \times Target) indicated that the initial directional variability was the same irrespective of the condition, $F(4, 20) = 1.9, p > .15$, or interaction, $F(12, 60) = 1.2, p > .25$, factors. Consistent evidence was obtained when hand path variability was considered. At the point where 50% of the movement distance had been covered, the characteristics of the confidence ellipses describing hand path variability were not significantly different. The first significant effect of the condition factor (simple effect or interaction) was found during the second part of the trajectory, when 54% of the total movement distance had been covered. At this point, the confidence ellipse started to be more elongated in the conditions allowing updating of the target location at the end of the saccadic shift (S-endE: 2.5; S-endH: 2.8) than in the conditions that did not (S-begE: 1.9; F-begH: 2.0; F-endH: 2.2). These results are illustrated in Figure 4.

Hand Kinematics: Trajectories Start Diverging Smoothly in the Updating Conditions After Hand Peak Acceleration

The main kinematic parameters were found to vary significantly only with target eccentricity. Peak acceleration, peak velocity, and

peak deceleration were of greater magnitude for larger movements. The time of occurrence of these different peaks was delayed when the target eccentricity was increased, $F_s(3, 15) > 15.7, p < .0001$. No effect of the condition factor, $F_s(4, 20) < 1.8, p > .15$, and no Condition \times Target interaction, $F_s(12, 60) < 0.7, p > .70$, was observed for these kinematic indicators.

The absence of significant variation between conditions of the main kinematic landmarks despite the existence of consistent modifications of the movement amplitude may appear puzzling at first glance. However, this result can be understood if one assumes that path corrections are smoothly distributed along the trajectory. In this case, feedback-related effects may be small relative to the intertrial variability, thus preventing identification of significant differences between conditions. Specific analyses were carried out to address this possibility. In these analyses, instantaneous velocities were summed up across a given interval, thereby favoring identification of global differences. (Differences that are too small to be detected statistically at each point of the curve may become sizable and thus identifiable when summed up over a time interval.) Three intervals were considered: from movement onset to peak acceleration, from peak acceleration to peak velocity, and from peak velocity to the end of the movement (deceleration phase). The results of these cumulative analyses are reported below and summarized in Figure 5.

From movement onset to peak acceleration. The measure of initial cumulative velocity, determined from movement onset to peak acceleration, was found to increase significantly and monotonically only as a function of the target eccentricity, $F(3, 15) =$

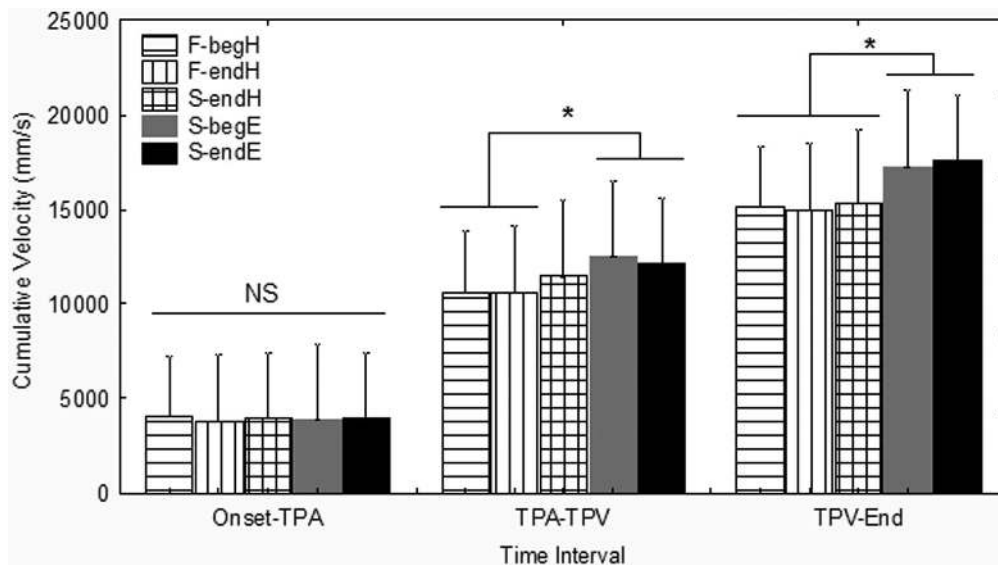


Figure 5. Variation of the instantaneous velocity summed over three different intervals for the five experimental conditions. The cumulative velocity is similar in all conditions for the first interval. It diverges after this instant: Cumulative velocity increases when updating of the target location is allowed at the end of the saccade (S-endE, S-endH). Asterisks indicate significant differences between the experimental conditions at the $p < .05$ level, and NS indicates nonsignificant differences. F-begH = fixation required, with target on until beginning of hand movement; F-endH = fixation required, with target on until end of hand movement; S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement; Onset-TPA = movement onset to peak acceleration; TPA-TPV = peak acceleration to peak velocity; TPV-End = peak velocity to the end of the movement.

66.4, $p < .0001$. No effect of the condition factor, $F(4, 20) = 0.3$, $p > .85$, and no Condition \times Target interaction, $F(12, 60) = 0.5$, $p > .85$, were identified. Of interest, the highest cumulative velocity was observed under the F-begH condition (4,027 mm/s), not under S-endE (3,899 mm/s) or S-endH (3,929 mm/s) conditions, as would be predicted if the longer movement amplitudes under those conditions were attributable to differences in feed-forward planning.

From peak acceleration to peak velocity. When the cumulative velocity was computed between the peak acceleration and the peak velocity, significant effects of both the target eccentricity, $F(3, 15) = 158.2$, $p < .0001$, and the experimental condition, $F(4, 20) = 6.3$, $p > .002$, were observed. There was no interaction between these two factors, $F(12, 60) = 1.2$, $p > .25$. As shown by post hoc analyses, the main effect of the condition factor was related to the fact that cumulative velocity was higher in S-endE (12,466 mm/s) and S-endH (12,414 mm/s) than in the two fixation conditions (F-begH: 10,553 mm/s; F-endH: 10,652 mm/s; $p < .01$). The difference with S-begE did not reach the statistical threshold (11,600 mm/s; $p > .10$).

From peak velocity to the end of the movement. When the cumulative velocity was computed between peak velocity and the end of the movement (deceleration phase), significant effects of both the target eccentricity, $F(3, 15) = 256$, $p < .0001$, and the experimental condition, $F(4, 20) = 8.1$, $p < .0005$, were observed, without interaction, $F(12, 60) = 1.3$, $p > .20$. As shown by post hoc analyses, the main effect of the condition factor was related to the existence of significant differences between the two experimental conditions allowing updating of the target location at the

end of the saccadic shift (S-endE: 17,245 mm/s; S-endH: 17,589 mm/s) and the three experimental conditions that did not (F-begH: 15,113 mm/s; F-endH: 14,956 mm/s; S-begE: 15,319 mm/s; $p < .005$). These three conditions were not different from each other ($p > .55$), nor were S-endE and S-endH conditions ($p > .55$).

In summary, the results above show that hand velocity was smoothly modulated after the peak acceleration of the movement in response to the updating of the target location at the end of the saccadic shift. This observation and the actual modulation of the hand trajectory in the updating conditions are illustrated in Figure 6 on the basis of individual movements.

Hand Path Shape: Path Curvature Does Not Vary Significantly as a Function of the Experimental Conditions

Figure 7 displays individual movement paths for 1 subject and mean movement paths averaged across all subjects for each target and each experimental condition. In accordance with previous studies (e.g., Desmurget, Jordan, et al., 1997; Flash & Hogan, 1985; Gordon et al., 1994; Morasso, 1981), it can be seen that hand movements are essentially straight irrespective of the movement magnitude and the experimental condition. A more accurate analysis indicates, however, that the movement paths exhibit slight variations as a function of the target location. The maximum movement curvature increases with the target eccentricity (T1: .014; T2: .018; T3: .020; T4: .022), $F(3, 15) = 5.1$, $p < .02$, as reported in previous studies (Desmurget, Jordan, et al., 1997; Desmurget et al., 1999; Prablanc & Martin, 1992). There was no influence of the experimental condition on this variable, $F(4,$

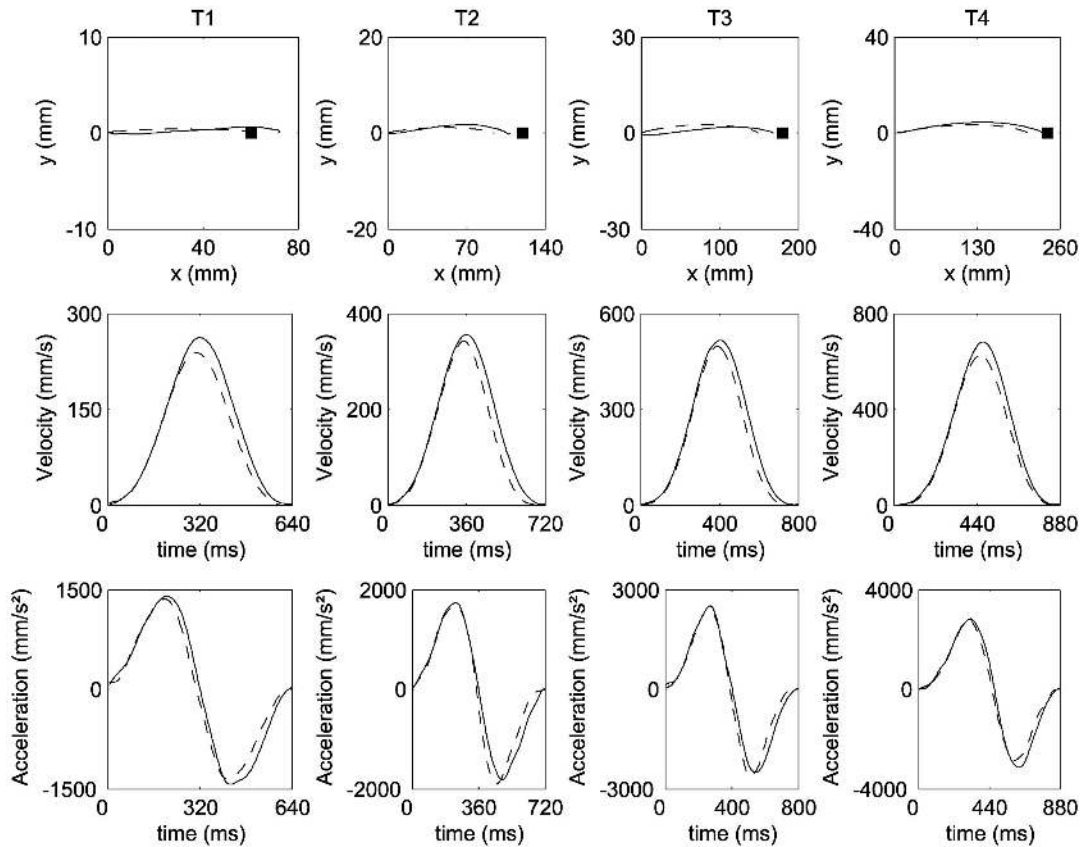


Figure 6. Representative individual trials recorded for all targets in the two conditions that respectively minimize (F-begH; dashed line) and maximize (S-endH; solid line) the amount of information available for feedback control. The first row shows hand paths. For the sake of clarity, these paths have been aligned along a common horizontal axis. Also, different scales have been used for the x- and y-axes. The black squares represent the target location. The second row shows the corresponding velocity profiles aligned on movement onset. The third row shows the acceleration profiles. As can be seen, movements were identical for a given target up to peak acceleration. They started to diverge smoothly after this instant. T = target; F-begH = fixation required, with target on until beginning of hand movement; S-endH = saccade permitted, with target on until end of hand movement.

20) = 0.5, $p > .70$, and no Condition \times Target interaction, $F(12, 60) = 1.7, p > .09$.

To analyze the shape of the hand path more precisely, we examined the level of path curvature on seven points equally distributed along the trajectory (see the *Method* section of this experiment). For all the points except the first and second ones, a significant influence of the target eccentricity was reported: The further the target, the more curved the movement, $F(3, 15) > 4.1, p < .03$. When the experimental condition, $F(4, 20) < 2.1, p > .10$, or the interaction, $F(12, 60) < 1.8, p > .07$, factors were considered, no significant influence was observed. In other words, we could not identify any variation in the degree of movement curvature as a function of the experimental conditions, anywhere along the hand path.

Taken together, the results above show that it was not possible to distinguish between the five experimental conditions on the basis of the shape of the hand paths. At first glance, this result may seem puzzling. Indeed, a change in the ongoing trajectory should induce substantial modifications of the movement curvature. This apparent discrepancy can be understood if one considers that

online feedback loops can cause the movement curvature to either increase or decrease. Figure 8 illustrates this point using the maximal curvature index. This figure shows four computationally generated movements: two reference paths presenting with identical curvature and two corrected paths identical to the reference paths during the initial 160 ms of the movement and different afterward. As is evident in the figure, the curvature of the corrected movements can be greater or less than the curvature of the reference movements. As a consequence, the mean movement curvature remains globally unaffected despite the existence of significant online modifications of the movement amplitude. Figure 8 also shows that the end-point scatter observed along the sagittal axis (directional variability) can decrease despite the absence of modification of the mean movement curvature index.

Hand Velocity Profiles: Corrected and Uncorrected Velocity Profiles Exhibit Similar Bell Shapes

Figure 6 displays individual velocity profiles for the two conditions that respectively minimize (F-begH) and maximize

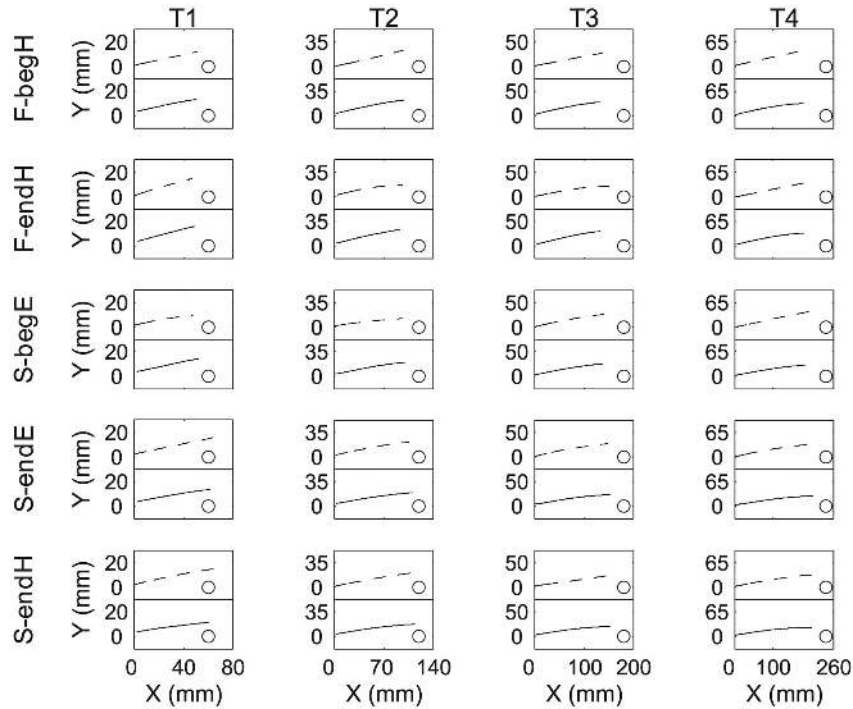


Figure 7. Individual movement paths for 1 subject (dashed line) and mean movement paths averaged across all subjects (solid line) for each target (open circles; T1–T4) and each experimental condition. Note that hand paths look fairly straight irrespective of the condition and target factors. F-begH = fixation required, with target on until beginning of hand movement; F-endH = fixation required, with target on until end of hand movement; S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement.

(S-endH) the amount of information available for feedback control. As can be seen in the figure, movement velocity presents a similar single-peaked, bell-shaped profile in both experimental conditions. Also, all velocity curves are smooth and devoid of corrective submovements. Quantitative analyses consistent with these claims are reported below.

A first analysis indicated that the number of individual responses exhibiting discrete submovements during the deceleration phase was low (less than 12%) and independent of the experimental conditions. In particular, the number of corrective submovements was not larger in the two updating conditions (S-endE, S-endH) than in the other three conditions (F-begH, F-endH, S-begE): main effect, $F(4, 20) = 2.4, p > .09$; interaction, $F(12, 60) = 1.4, p > .15$. This result suggests that the higher accuracy observed in S-endE and S-endH with respect to the other conditions is not due to the generation of discrete corrective responses

during the deceleration phase. This conclusion agrees with the observation that hand trajectory is affected between peak acceleration and peak velocity when vision of the target is allowed at the end of the saccadic shift (see above). Also, it is coherent with the fact that the kinematic and spatial results reported in the sections above remain unchanged when the trials presenting with discrete submovements are removed.

Specific analyses were carried out to identify systematic variations of the shape of the velocity profiles as a function of the experimental conditions. These analyses indicated that the symmetry indexes were close to .50 for all conditions and all target eccentricities. Movement symmetry was not significantly affected by the condition factor (F-endH: .48; F-begH: .49; S-begE: .49; S-endE: .48; S-endH: .47), $F(4, 20) = 2.2, p > .09$, and no Target \times Condition interaction was observed, $F(12, 60) = 0.8, p > .65$. This result indicates that the durations of the acceleration and deceleration phases were roughly equivalent, irrespective of the experimental manipulations. An absence of effect of the experimental factors was also observed when the global shape index was considered. As shown in previous reports, if two velocity profiles have different shapes, the ratio of the peak velocity to the average velocity varies consistently (Novak et al., 2000; Soechting, 1984). Our data did not reveal any significant variation of this ratio as a function of the condition (F-endH: 1.6; F-begH: 1.6; S-begE: 1.7; S-endE: 1.7; S-endH: 1.7), $F(4, 20) = 1.9, p > .10$, or the interaction, $F(12, 60) = 1.5, p > .10$, factors. A consistent conclusion was reached on the basis of the shape anal-

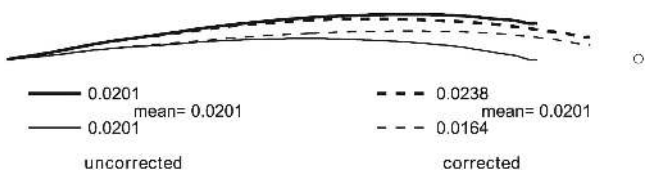


Figure 8. Four computationally generated movements: Two reference paths with identical curvature indexes (solid lines) and two corrected paths (dashed lines). These corrected paths are identical to the reference paths during the 160 ms of the movement and different afterward.

ysis. The similarity index computed by comparing each normalized velocity profile to a reference curve (see the *Method* section of this experiment) was not affected by the condition, $F(4, 20) = 1.7, p > .15$, the target, $F(3, 15) = 2.4, p > .10$, or the interaction, $F(12, 60) = 0.8, p > .65$, factors. The same results were obtained when the symmetry, the global shape, and the similarity indexes were determined after removal of the responses presenting with discrete corrective submovements.

In summary, the data above show that a gradual change in movement amplitude can occur without major (i.e., statistically identifiable) changes in the shape of the velocity profiles.

Contrasting Hand and Eye Accuracy: Hand and Eye Final Variability Are Unrelated

Two elements presented in the previous sections seem to indicate that gaze location does not represent a target signal toward which hand movement is attracted. First, movement accuracy was not significantly different in the fixation conditions (F-endH, F-begH) and in S-begE. Second, in S-endE and S-endH, a variation of the end-point accuracy as a function of the target eccentricity was observed for hand movement but not for eye movement.

In light of the previous results, additional analyses were carried out to directly test the hypothesis that the gaze axis is not used as a control signal for guiding the hand to the target. In these additional analyses, we investigated the possibility that eye and hand amplitude variabilities did change concurrently. To this end, we computed for each subject, each experimental condition, and each target the ratio of the eye amplitude standard deviation to the hand amplitude standard deviation (see the *Method* section of this experiment). This ratio was not affected by the target factor, $F(3, 15) = 1.7, p > .20$. It was, however, significantly influenced by the condition factor, $F(2, 10) = 16.2, p < .001$. As shown by post hoc analyses, this ratio was higher in S-begE (0.114) than in S-endH (0.066; $p < .001$) and S-endE (0.058; $p < .002$). No significant difference was observed between the two latter conditions ($p > .50$). As can be seen in Figure 9, the variation of this ratio as a function of the experimental conditions can be largely explained by significant differences in the final gaze variability as a function of the experimental condition (S-begE: 1.12° ; S-endE: 0.51° ; S-endH: 0.54°), $F(2, 10) = 227.5, p < .0001$. This difference contrasts with the absence of variation of the hand final variability (S-begE: 11.0 mm; S-endE: 9.9 mm; S-endH: 9.7 mm), $F(2, 10) = 1.3, p > .30$. The latter result is consistent with the absence of a significant effect of the condition factor on the long axis of the end-point confidence ellipse (this axis was aligned with the mean movement direction).

In summary, the results above indicate that an increase of the gaze amplitude variability is not accompanied by a concomitant increase of the hand amplitude variability. In this study, hand extent variability was the same for the three experimental conditions, irrespective of the changes observed for gaze variability.

Correlation Analyses: Initial Kinematics Poorly Predicts the Movement End Point

As reported above, the duration and maximal magnitude of the hand acceleration increase with the target eccentricity. These two variables exhibit a quasi-linear augmentation when expressed as a function of the target factor (peak acceleration—T1: 794 mm/s^2 ;

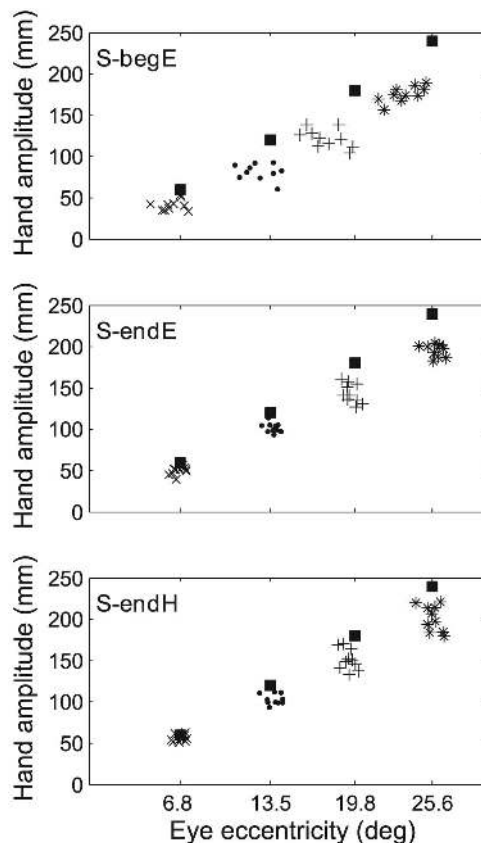


Figure 9. Eye amplitude versus hand amplitude for a representative subject. Data are shown for all conditions that involved a saccadic response (S-begE, S-endE, S-endH) and for all target eccentricities ($\times = T1$; $\bullet = T2$; $+ = T3$; $* = T4$). The solid squares represent the target locations. S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement; deg = degrees.

T2: $1,159 \text{ mm/s}^2$; T3: $1,436 \text{ mm/s}^2$; T4: $1,755 \text{ mm/s}^2$; duration of the acceleration phase or time to peak velocity—T1: 264 ms; T2: 340 ms; T3: 373 ms; T4: 405 ms). This well-known association (Gordon et al., 1994; Messier & Kalaska, 1999; Schmidt et al., 1979) suggests strongly that the characteristics of the movement acceleration phase predict movement amplitude with fairly good accuracy. In light of this observation, however, one may wonder how good this prediction becomes at the single trial level. To address this issue, we investigated whether the final variance in movement amplitude could be predicted on the basis of the initial variance in movement acceleration (peak and duration; see the *Method* section of this experiment). On average, the prediction was better for the three conditions that did not allow any updating of the target location at the end of the saccadic shift (F-begH: $R^2 = .56$; F-endH: $R^2 = .50$; S-begE: $R^2 = .50$; mean $R^2 = .52$) than for the two conditions that did (S-endE: $R^2 = .35$; S-endH: $R^2 = .34$; mean $R^2 = .35$). When updating of the target location at the end of the saccadic shift was impossible, the initial variance in movement acceleration was able to account for more than 52% of the final variance in movement amplitude. The accuracy of this prediction was substantially smaller in the conditions that did allow target

updating. In this case, only 35% of the final variance in movement amplitude was predicted by the initial variance in movement acceleration. This value is close to the values reported in previous related studies (Fisher et al., 2000; Messier & Kalaska, 1999).

The fact that substantially weaker correlations were observed in the updating conditions is consistent with kinematic data showing that the ability to reestimate the target location at the end of the ocular saccade results in a substantial modification of the movement magnitude (see above). Another explanation might be that correlation coefficients are biased by the fact that movement amplitude is higher in the conditions allowing updating of the target location at the end of the saccadic shift. This explanation seems unlikely, however. Indeed, the amount of final variance in movement amplitude explained by the initial variance in movement acceleration decreased substantially as a function of the target eccentricity for all the conditions. This effect is smaller than the effect of the condition factor (especially when the first three targets are considered). This observation is inconsistent with the idea that slight differences in movement amplitude account for the differences observed between the experimental conditions. It is tempting to speculate that the progressive decrease of the correla-

tion coefficient as a function of the target eccentricity is related to the fact that feedback loops are more likely to affect movements of longer durations and amplitudes. The percentage of final variance in movement amplitude explained by the initial variance in movement acceleration is reported in Figure 10 for all conditions and all target eccentricities.

In the results above, we have shown that movement amplitudes started to diverge across the different experimental conditions between the time to peak acceleration and the time to peak velocity. However, our data did not provide evidence that movement amplitude was modulated in S-endH and S-endE by delaying time to peak velocity. Indeed, time to peak velocity was not significantly affected by the condition factor (see above). When time to peak velocity was compared across the different conditions, there was no trend suggesting that the conditions presenting with the largest movement amplitudes exhibited the longest acceleration phases (S-endH: 338 ms; S-endE: 352 ms; S-begE: 349 ms; F-begH: 351 ms; F-endH: 338 ms). This observation suggests that the duration of the acceleration phase was not affected by the feedback process and thus that this measure can be used reliably as a regressor in the analyses aiming to determine the contribution of

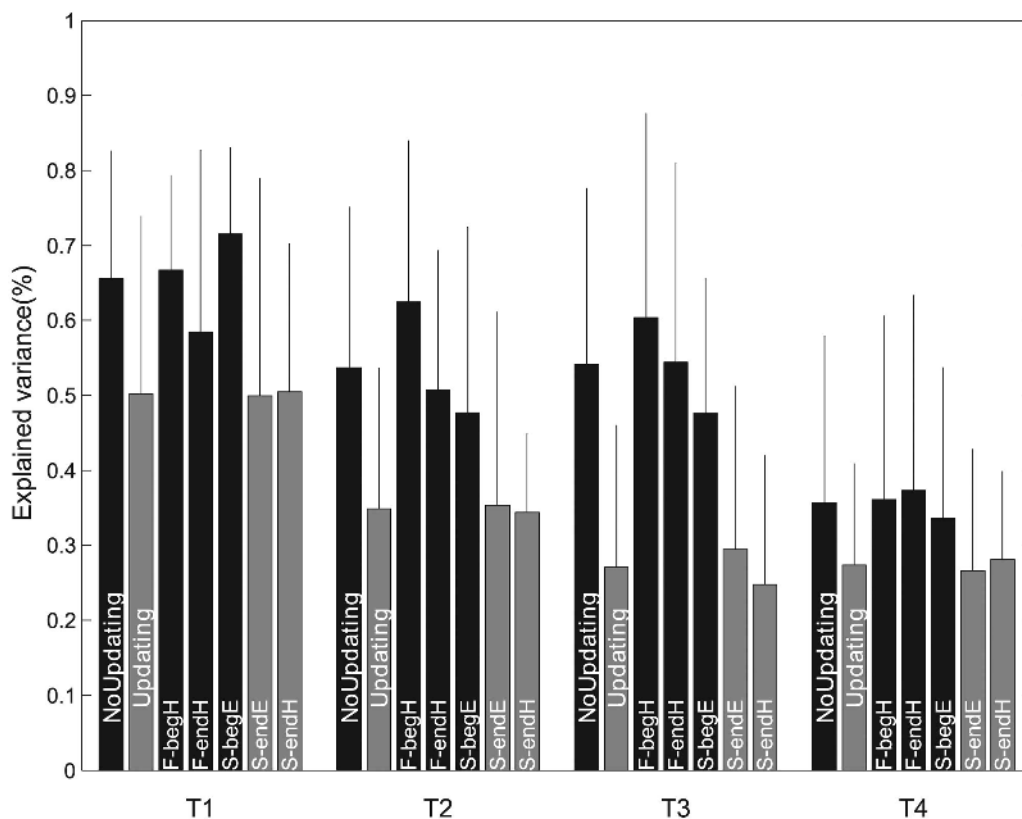


Figure 10. Percentage of final variance in movement amplitude explained by the initial variance in movement acceleration (magnitude and duration) for each condition and each target eccentricity (T1–T4). Vertical error bars represent standard deviations. NoUpdating = mean of the three conditions that did not allow updating of the target location at the end of the saccadic shift (F-begH, F-endH, S-begE). Updating = mean of the two conditions that did allow updating of the target location at the end of the saccadic shift (S-endE, S-endH). F-begH = fixation required, with target on until beginning of hand movement; F-endH = fixation required, with target on until end of hand movement; S-begE = saccade permitted, with target on until beginning of eye movement; S-endE = saccade permitted, with target on until end of eye movement; S-endH = saccade permitted, with target on until end of hand movement.

movement preplanning to movement amplitude. However, in the absence of definitive evidence that time to peak velocity is unaffected by feedback processes, we performed a more stringent analysis in which we correlated the final variance in movement amplitude with the variance in the early characteristics of hand acceleration (peak acceleration and time to peak acceleration; see the *Method* section in this experiment). The results were consistent with the ones obtained with time to peak velocity, except that the correlation values were smaller. On average, the prediction was better for the three conditions that did not allow any updating of the target location at the end of the saccadic shift (F-begH: $R^2 = .34$; F-endH: $R^2 = .40$; S-begE: $R^2 = .33$; mean $R^2 = .36$) than for the two conditions that did (S-endE: $R^2 = .27$; S-endH: $R^2 = .29$; mean $R^2 = .28$). In addition, there was a trend for the correlation coefficients to decrease as a function of the target eccentricity irrespective of the experimental condition.

Longitudinal Analyses: Learning Effects Cannot Account for the Significant Differences Between the Different Conditions

There were only four targets in the present experiment, and each experimental condition was presented in a separate session. It is possible that the subjects progressively learned the target locations, and thus order effects could have interfered with our results. Although we cannot reject this possibility, it appears very unlikely that our main observations reflect a learning effect of this sort. Indeed, the different conditions were randomly ordered across subjects, and it is difficult to envisage how such a random presentation could have generated systematic differences between the experimental conditions. To substantiate this claim, we conducted several analyses. We first tested the possibility that movement amplitude was different at the beginning and at the end of a given session. To this end, the early and late amplitude errors were computed by averaging the first two and last two trials of the session. A three-way ANOVA with repeated measures was then computed with condition (five levels), target (four levels), and order (two levels: early, late) as the factors. The order effect had no significant influence on the amplitude errors (main effect and interaction factor, $p > .30$). In a second step, the same analysis was conducted, but the condition factor was replaced by the session factor (five levels). In this case, the question was dual: (a) Do we observe a modification of the mean systematic error during the first, second, third, fourth, and fifth experimental sessions, and (b) do we observe a difference from session to session? Results failed to support these two hypotheses. The main and interaction effects involving the order factor did not reach the significance level ($p > .55$). This suggests that there was no learning effect within any session. At the same time, there was no sign that the between-sessions periods might have favored any kind of learning. Indeed, the main and interaction effects involving the session factor were also far from reaching the significance level ($p > .55$).

In addition to the investigations above, we conducted an additional test on a subset of data. For 3 subjects, the first and last sessions were sessions that did not allow updating of the target location at the end of the saccadic shift. Because these sessions were identical, we reasoned that they could be used effectively to determine the existence of a potential learning effect. For the 3 subjects who started and concluded the experiment with non-updating sessions, we used a two-way ANOVA (session: two

levels, first and last; eccentricity: four levels) to identify time-dependent variations of the movement amplitude. Results failed to show any effect of the session factor (session factor and interaction effects, $p > .90$). When the first and last sessions were compared, there was not even a trend suggesting that movement amplitude could have changed during the experiment (first session: -25.1 mm; last session: -24.5 mm).

Discussion

In summary, there are six main results in this first experiment. First, when updating of the target location is allowed at the end of an orienting saccade, end-point systematic errors and end-point directional variability are decreased. Second, hand trajectories are identical in all conditions up to the time of peak acceleration. Third, trajectory corrections occur smoothly between peak acceleration and the end of the movement, in agreement with the hypothesis that movement amplitude is modulated online through feedback mechanisms. These smooth corrections cause the corrected and uncorrected velocity profiles to exhibit similar bell shapes. Fourth, errors are corrected without modification of the movement straightness. Fifth, the final variance in movement amplitude cannot be robustly predicted on the basis of the initial variance in movement acceleration, even when the external signals potentially available for feedback control are minimized (F-begH). This suggests that target updating is not the only critical input for feedback control. Sixth, hand and eye final positions do not correlate with each other, suggesting that gaze direction does not serve as a target signal for arm motor guidance. These results are briefly discussed below.

The Ability to Update the Location of the Target at the End of the Saccade Improves Movement Accuracy

The present experiment shows that the accuracy of simple reaching movements is significantly improved when the motor system has the opportunity to reestimate the location of the target at the end of the saccadic shift. This improvement includes reductions in both the systematic and variable errors. Regarding systematic errors, we found that movement amplitude was increased by 10%, on average, when updating of the target location was allowed at the end of the saccadic shift. No modification of the movement direction was observed. These results agree with other studies showing that target eccentricity tends to be underestimated by the peripheral retina (Bock, 1993; Prablanc et al., 1979, 1986). Also, they are compatible with the fact that visual saccades exhibit generally consistent amplitude errors without noticeable directional biases (Becker, 1991; White, Sparks, & Stanford, 1994). With respect to this point, it is worth noting that the absence of an effect of the experimental condition on the direction error could have been favored, in the present study, by the frontoparallel nature of the movements that were investigated. Indeed, the fixation point and the target diode were presented along the same retinal meridian, thus facilitating estimation of the target meridional eccentricity. In addition, the subjects were aware that the movements were performed along a frontoparallel line.

The Ability to Update the Location of the Target at the End of the Saccade Decreases Direction Variability

Regarding variable errors, we found that the area of the movement-end-point confidence ellipse was decreased by almost

55% when updating of the target location was allowed at the end of the saccadic shift. Although expected, this decrease was surprising in its nature. Indeed, it did not affect all of the dimensions of the motor response but was mostly restricted to the directional component of the movement. In other words, when the subjects had the opportunity to reestimate the location of the target at the end of the saccadic shift, a substantial part of the directional variability of the movement was amended without concomitant modification of the extent variability. Elucidation of this effect is not straightforward. A first (unlikely) explanation is perceptual. According to this explanation, the variability in estimating the target location would be reduced in the foveal area with respect to the peripheral retina for the radial eye axis only (i.e., the axis orthogonal to the movement direction in the present study). No reduction would be observed for the meridional axis (i.e., the axis collinear with the movement direction in this study). This hypothesis is not supported by the homogeneity of the retinal structure and by the fact that saccadic variability is close to zero, for small saccades, in both the radial and meridional directions (Becker, 1991; Lemij & Collewyn, 1989). It is also incompatible with the observations of the second experiment (see below).

An alternative explanation might be related to the existence of complex interactions between the perceptual and motor sources of noise. If the motor variability associated with the planning (or the control) of the movement is large with respect to the perceptual variability associated with the estimation of the target location, then decreasing this second variability will have a limited impact on the movement final accuracy. In other words, the smaller the motor variability, the greater the effect of decreasing the perceptual variability. Within this context, our data can be explained under the assumption that the variability in planning (or controlling) the required movement direction is smaller than the variability in planning (or controlling) the required movement extent. If such is the case, a homogeneous decrease of the variability in estimating the target position would be expected to have a larger impact on movement direction than on movement extent, thus leading to a modification of the shape of the end-point confidence ellipse. Beyond this speculation, it is worth mentioning that the influence exerted by target capture on the movement final variability raises questions about the interpretation of several studies that made inferences about the processes of advanced planning of movement from the pattern of end-point variability (Desmurget et al., 1999; Desmurget, Prablanc, & Rossetti, 1997; Gordon et al., 1994; Messier & Kalaska, 1997; Vindras & Viviani, 1998).

Movement Amplitude Is Smoothly Modulated Through Feedback Mechanisms

With respect to the results above, a major issue concerns the origin of the differences observed between the experimental conditions. Two main hypotheses can be proposed: The origin is feedforward planning, in which the movement is planned after reestimation of the target location, that is, after completion of the saccadic shift, or the origin is the use of feedback loops, in which the movement is planned before reestimation of the target location, that is, before completion of the saccadic shift. In the first case, the changes in movement amplitude would be associated with the existence of different initial motor commands for each condition (e.g., increased or lengthened initial acceleration). By contrast, in the second case, the initial motor command would be the same for

all conditions, and the changes in movement amplitude would be associated with an online modulation of this initial command. Two arguments support this second hypothesis. First, the overt hand movement was detected a few tens of milliseconds after completion of the saccadic shift (between 31 and 77 ms, depending on the target eccentricity). This latency seems too short to be compatible with the idea that hand movements were fully replanned, on the basis of an accurate estimation of the target location, after completion of the saccadic shift. The issue of limb inertia makes this conclusion even more compelling. Indeed, several studies have established that limb inertia causes the actual hand movement to lag muscle contraction by more than 100 ms (Biguer et al., 1982; Godaux et al., 1992; Turner et al., 1995). Second, our data indicate that hand movements exhibit similar characteristics, in all conditions, up to peak acceleration. Kinematic divergence starts to emerge only after this instant.

If one admits, on the basis of the evidence above, that the initial underestimation of the target eccentricity by the peripheral retina is corrected through feedback mechanisms, the present study has three main implications. First, point-to-point movements performed without vision of the limb cannot be considered ballistic despite the fact they follow a roughly straight path and exhibit a smooth, bell-shaped velocity profile (see the introduction). Our data suggest that path corrections are not always associated with kinematic discontinuities and zero crossings of the acceleration profiles. This result extends and generalizes the conclusions of previous studies in which smooth path corrections were observed in response to subliminal target jumps triggered during the saccadic response (Goodale et al., 1986; Pélisson et al., 1986; Prablanc & Martin, 1992). Second, the insensitivity of commonly used measures of movement kinematics to substantial modifications of the movement amplitude can explain the remarkable ability of purely feedforward models to fit the main kinematic characteristics of point-to-point movements (Flash, 1987; Flash & Hogan, 1985; Harris & Wolpert, 1998; Plamondon & Alimi, 1997; Uno et al., 1989). As shown in the present study, a 10% increase of the movement amplitude affected only marginally the straightness of the hand paths and the shape of the velocity profiles. Third, it is probably misleading to make inferences about the feedforward processes of movement planning based on the pattern of end-point errors. Indeed, not only the area but also the shape of the end-point variability can apparently be influenced by feedback mechanisms.

The Final Variance in Movement Amplitude Cannot Be Robustly Predicted on the Basis of the Initial Variance in Movement Acceleration

In summary, the data above suggest that errors related to misestimation of the initial target location are corrected online. Of interest, this is apparently not the only source of inaccuracy that can be processed during the movement. As shown by correlation analyses, it was not possible in the present study to robustly predict the final variability in movement amplitude on the basis of the early variability in movement acceleration, even when errors in target localization were eliminated (at best, correlation analyses captured around 55% of the final movement variance). This result confirms previously published observations (Fisher et al., 2000; Messier & Kalaska, 1999). Although the nature of the additional errors observed in this study cannot be directly identified, we would like to speculate that they represent mainly execution errors.

In other words, we hypothesize that the modest correlations observed for a given target location between the initial characteristics of the acceleration vector and the movement amplitude reflect the existence of a feedback loop involving a comparison between the actual and expected proprioceptive feedback signals (Shergill, Bays, Frith, & Wolpert, 2003). This hypothesis is structured around two main ideas. First, the proprioceptive input is the only signal available to detect an ongoing error in the F-begH condition: When vision of the moving limb is prevented, only proprioception can signal that the hand is not where it is supposed to be and/or that the motor command does not have the expected effect. Second, during movement, proprioception apparently does not supply the motor system with an absolute signal (e.g., limb posture) but with relative information (rate of change in muscle length; Gandevia & Burke, 1992; Hulliger, 1984; Matthews, 1981; but see Kakuda & Nagaoka, 1998). In other words, the proprioceptive signal that is generated by the muscle spindles does not indicate the actual state of the motor system but rather its current state with respect to its previous (and original) state. As a consequence, if an incorrect muscle command is selected (e.g., an underestimated gain) and/or if the initial posture of the limb is erroneously estimated prior to movement onset, the motor system has no way to perceive it. By contrast, if the executed movement does not exactly match the planned one, an error signal is accessible, due to the existence of a detectable difference between the sensed and expected rate of change in muscle length.

In agreement with these claims, behavioral results have shown that modifying the expected output of muscle spindles, through vibration, during the ongoing movement causes systematic misreaching (Capaday & Cooke, 1981; Kasai, Kawanishi, & Yahagi, 1992; Redon, Hay, & Velay, 1991). At the same time, evidence has been provided that errors in the estimation of either the force to be generated to reach the target and/or the initial state of the motor apparatus are not amended during the movement. For instance, an overscaled initial acceleration has been found to result in large uncompensated overshoots in control subjects (Vindras & Viviani, 1998). Similarly, a systematic underscaling of the initial electromyogram burst in patients with Parkinson's disease has been demonstrated to result in uncompensated undershoots (Desmurget et al., 2003). Other studies have demonstrated that biases in the estimation of the initial state of the motor apparatus are reflected precisely in end-point accuracy during point-to-point movements (Bock & Eckmiller, 1986; Brown, Rosenbaum, & Sainburg, 2003; Rossetti, Desmurget, & Prablanc, 1995; Sainburg, Lateiner, Latash, & Bagesteiro, 2003; Vindras et al., 1998).

Gaze Direction Does Not Serve as a Target Signal for Arm Motor Guidance

An interesting result of the present experiment concerns the potential role of gaze direction for movement control. Our data show the following: (a) Movement is not more accurate when gaze is directed at the vicinity of the target (i.e., fixation conditions vs. S-begE). (b) Variation of the amplitude error as a function of target eccentricity exists only when the primary saccadic response is considered. When the target remains visible at the end of the initial saccadic shift (i.e., when a corrective saccade is generated: S-endE, S-endH), an eccentricity-related effect persists for hand movements (hypometria increases with the target eccentricity) but not for eye movements. (c) An increase in gaze amplitude vari-

ability is not accompanied by a concomitant increase in hand amplitude variability. When considered together, these results do not support the idea that gaze direction serves as a target signal for arm motor control. This conclusion is consistent with several other main lines of evidence. First, although the gaze location is always accurately anchored on the target, when the target is present, an eccentricity-related effect is generally observed for hand movements performed without vision of the moving limb (for a review, see Jeannerod, 1988; Keele, 1968). Second, after saccadic adaptation, hand reaching movements are only marginally affected (Krolller, De Graaf, Prablanc, & Pélissier, 1999). Third, human subjects' performance is very poor when pointing with their unseen hand to where they look, either in the dark or when gazing at a visual target (Blouin, Amade, Vercher, Teasdale, & Gauthier, 2002; Blouin, Gauthier, & Vercher, 1995). Fourth, eye and hand accuracies vary differently across various experimental situations (Sailer, Eggert, Ditterich, Hassenzahl, & Straube, 2003; Sailer, Eggert, Ditterich, & Straube, 2000). Fifth, eye and hand variabilities do not correlate for reaching movements performed at actual or memorized targets (Biguer, Prablanc, & Jeannerod, 1984; Delreux, Vanden-Abee, Crommelinck, & Roucoux, 1991; Prablanc et al., 1979; Sailer et al., 2000).

The results of the present experiment offer an alternative explanation to the conclusion of several studies recently published in the literature. In these studies, a correlation between the errors in hand and gaze final locations was reported for movement directed at memorized targets (Enright, 1995; Flanders et al., 1999) or at the predicted location of a moving target (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002; Soechting et al., 2001). Such a correlation was also observed in the present study for a condition in which the target was turned off at saccadic onset (S-begE). When the target remained present until the end of the saccade (S-endE) or the end of the hand pointing movement (S-endH), this correlation was no longer present. This suggests that the association between the eye and hand errors for movements directed at absent targets (memorized, turned off, or predicted) might reflect the fact that the gaze and arm control systems are affected, during motor planning, by a commonly biased estimation of the target location by the peripheral retina. The absence of correlation between the noise inherent to each of the arm and eye systems supports this claim. Indeed, for the S-begE condition, the positive correlation observed between the eye and hand final locations is only present at the intertarget level. This correlation disappears when statistical analyses are carried out for each target separately. Also, for S-begE, the increase in eye final variability with respect to S-endH is not associated with a concomitant increase of the hand final variability.

Before concluding this section, it may be worth discussing the observation that reaching movements were equally accurate in two conditions in which the eyes were either free to move (S-begE) or locked at a central fixation point (F-begH, F-endH). Indeed, several studies have suggested that preventing eye motion led to a decrease in movement accuracy (Abrams, Meyer, & Kornblum, 1990; Enright, 1995; Prablanc et al., 1979; Vercher, Magenes, Prablanc, & Gauthier, 1994). With respect to this discrepancy, one may note that the study in the parenthetical list that is the closest to ours, in terms of the experimental design, is the one by Prablanc et al. (1979). In this study, significant differences between the fixation and S-begE conditions were observed only for movements that were larger than 300 mm. For movement located in the range

of amplitude used in the present study, no significant differences in end-point accuracy were reported. Also, in our study, the ability to see the hand prior to movement onset, in the pointing plane, along the same radial line as the target line, is likely to have improved the subjects' ability to estimate the location of the target relative to the hand.

Experiment 2: Modulating Movement Direction

In this second experiment, we studied reaching movements for which the hand and eye responses were performed, in the dark, along quasi-orthogonal directions. As in the first study, we manipulated the ability of the subjects to update the target location at the end of the saccadic shift. In contrast to the first experiment, however, the different conditions were randomized within a single session. Also, more targets were used ($n = 7$). These last two changes were implemented to minimize the risks of strategic control and motor learning. This second experiment was conducted to pursue three main goals. First, we aimed to provide indisputable evidence that reestimation of the target location affects movement accuracy through feedback control. To this end, larger saccadic responses were studied with the purpose of making it easier to determine whether the hand starts moving before completion of the saccadic shift. Also, directional corrections were investigated that should allow reliable determination of the instant when the different experimental conditions start diverging. The second goal of this study was to evaluate the potential contribution of early errors in localizing the target on movement curvature. Addressing this question is important with respect to the long-lasting controversy about the origin of path curvature during visually directed movements (Flash, 1987; Haggard & Richardson, 1996; Nakano et al., 1999; Rosenbaum et al., 1995; Uno et al., 1989; Wolpert, Ghahramani, & Jordan, 1994; for a review, see Desmurget et al., 1998). Finally, the last goal of this study was to generalize the results of the first experiment from 2-D constrained movements to 3-D unconstrained movements. This might be an important issue considering that constrained and unconstrained movements have been suggested to rely on different control processes (Desmurget, Jordan, et al., 1997; Desmurget et al., 1999).

Method

Subjects

Five subjects (2 men and 3 women, ages 21–38 years) participated in this experiment, after their informed consent was obtained. They were all free of neurological deficits, right-handed, and naive about the purpose of the study. The experimental procedure was approved by the Human Investigations Committee of our institution.

Apparatus

A schematic representation of the experimental apparatus used in the present study is presented in Figure 1. This apparatus is similar to the one used in the first experiment except for the target locations and for the fact that movements were recorded in 3-D with a magnetic system (see below). The hand starting position (S') was located, in the sagittal direction (y -axis), 200 mm in front of the subject's eye plane. Eight LEDs (1 green, 7 red) were positioned along a frontoparallel line (x -axis). The sagittal distance of the target line to the hand starting position was 300 mm. The green LED was located 160 mm to the left (gaze fixation target). The red LEDs were positioned to the right at 160 mm (T1), 180 mm (T2), 200 mm

(T3), 220 mm (T4), 240 mm (T5), 260 mm (T6), and 280 mm (T7). During the experiment, the subject's head was fixed with a chin rest and positioned along the line joining the hand starting point to the fixation target. The chin rest was adapted to position the eyes 40 cm above the table. When expressed in eye coordinates, the target eccentricities were thus, gaze fixation target: -14.0° ; T1: 14.0° ; T2: 15.7° ; T3: 17.4° ; T4: 19.0° ; T5: 20.6° ; T6: 22.1° ; and T7: 23.6° .

Experimental Conditions and Procedure

The procedure was the same as in the first experiment. On the basis of the results of this first experiment, only two experimental conditions were selected for this second study: S-endH—saccade permitted, with target on until end of hand movement; S-begE—saccade permitted, with target on until beginning of eye movement. These two conditions were presented in a single session. Each subject performed 140 trials (7 targets \times 10 repetitions \times 2 conditions). The different target locations and different experimental conditions were randomly intermixed within the session. The subjects were instructed to "point as accurately as possible with a single uncorrected movement." They were free to lift the fingertip above the table.

Movement Recording and Data Analysis

Movement of a small sensor located on the subject's index fingertip was recorded with a magnetic tracking system (miniBIRD; Ascension Technology Corporation, Burlington, VT) at a sampling frequency of 100 Hz. Horizontal eye movements were recorded with an infrared optometric system (EyeLink tracker; SR Research, Mississauga, Ontario, Canada) at a frequency of 250 Hz. The procedure for data analysis was the same as that in the first experiment. However, an additional test was carried out to identify the time at which horizontal movement directions (i.e., the orientation of the velocity vector in the pointing plane) started to diverge between the S-endH and S-begE conditions. Movement direction was computed for every point of each trajectory (i.e., every 10 ms) between 50 and 350 ms (path corrections, if any, are expected to fall within this time interval; Desmurget et al., 2004; Desmurget & Prablanc, 1997; Prablanc & Martin, 1992; see Desmurget & Grafton, 2003, for a review). The individual values were then averaged for each subject, each condition, and each target. For each point, a two-way ANOVA with repeated measures was computed (Condition \times Target). The instant of path divergence was defined as the first point for which the instantaneous movement direction was significantly affected by the condition factor.

Results

In the following, only the results that expand or contradict the observations of the first experiment are presented in detail.

Eye-Hand Coordination: Arm Motor Command Is Issued Prior to Saccade Completion

On average, RT_{eye} was equal to 205 ms. This variable was not affected by any of the experimental factors (all $ps > .50$). A different pattern of variation was observed for MD_{eye} . On average, MD_{eye} was equal to 124 ms. This parameter was found to vary only as a function of the target eccentricity from 114 (T1) to 136 (T7) ms, $F(6, 24) = 20.0$, $p < .0001$.

On average, RT_{hand} and MD_{hand} were equal to 325 and 568 ms, respectively. None of these variables was found to depend on the experimental factors (all $ps > .20$).

The previous results indicate that hand movement onset occurred around the end of the saccadic shift. Small variations were observed due to variability in both eye and hand reaction time and

due to the fact that MD_{eye} increased with movement amplitude. The hand started moving within an interval ranging from 15 ms after (T2) to 23 ms before (T7) saccadic completion. These values are consistent with previous studies involving similar paradigms (Desmurget et al., 2001, 2004; Prablanc & Martin, 1992). They support the idea that arm movements were planned and initiated before completion of the primary saccadic response, that is, before updating of the estimation of the target location by foveal vision.

Eye Movements Accuracy: A Corrective Saccade Allows Proper Target Foveation in the Updating Condition

The saccadic responses were similar to the ones observed in the first experiment. In the S-endH condition, most responses consisted of two phases: an initial saccade undershooting the target position and covering, on average, 91% of the required displacement and a corrective saccade achieving accurate target foveation. Corrective saccades were present only in a minority of trials in the S-begE condition (<10%), as reported in the first experiment and previous studies (Prablanc & Jeannerod, 1975; Prablanc et al., 1986). For S-begE, the magnitude of the primary saccadic response (91%) was not statistically different from the magnitude of the final gaze location (91%).

Hand Accuracy: Direction Errors Are Reduced in the Updating Condition

As can be seen in Figure 11, end-point accuracy was clearly different in the two experimental conditions. In particular, the movement end point was perceptibly shifted to the right in S-endH with respect to S-begE. This shift amounted to 1.6° on average, which represents 5% of the mean saccadic displacement. The change in movement end point accounts for the significant influence of the condition factor on the direction error (S-endH: 0.7° ; S-begE: 2.25°), $F(1, 4) = 118.3, p < .0005$. This influence was constant for the different target eccentricities, as shown by the absence of a Condition \times Target interaction, $F(1, 4) = 1.1, p > .40$. Amplitude error did not show any modification as a function of the experimental factors (all $ps > .75$).

Hand Accuracy: Variable Errors Are Reduced Isotropically in the Updating Condition

A modification of the area of the end-point confidence ellipse was observed as a function of the condition factor, $F(1, 4) = 10.1, p < .04$. The confidence area was 24% smaller in S-endH ($1,003 \text{ mm}^2$) than in S-begE ($1,312 \text{ mm}^2$), suggesting that end-point variability could be substantially reduced when the subject had the opportunity to update the location of the target at the end of the saccadic shift. In contrast to the results of the first experiment, however, we did not find this reduction to be accompanied by a significant modification of the shape of the end-point confidence ellipse. The ratio of the major to the minor axis of the end-point cluster was not statistically different in S-begE (1.80) and S-endH (1.93), $F(1, 4) = 1.4, p > .30$. To enlighten this discrepancy, we feel it may be worth mentioning that the end-point clusters tended to be less elongated and less consistently aligned with the mean movement direction in this second study. This result, reported in previous reports (Desmurget, Jordan, et al., 1997; Desmurget et al., 1999), is illustrated in Figure 12.

Hand Path Shape: Path Curvature Increases Significantly in the Updating Condition

As shown in Figure 11 (top panel), 3-D hand paths were consistently curved, due to the fact that the subjects lifted their hands above the table while pointing. Neither the time of occurrence nor the maximal amount of vertical deviation were significantly affected by the experimental factors (all $ps > .05$). As shown by a detailed analysis of the data, all the significant differences between the experimental conditions were identified in the horizontal plane. When expressed in this plane, hand paths presented a slightly curved shape (see Figures 11 and 12). As reported in previous studies (Desmurget et al., 2004; Prablanc & Martin, 1992), the amount of curvature increased slightly with target eccentricity (T1: 0.040; T7: 0.067), $F(6, 24) = 15.5, p < .0001$. A significant effect of the condition factor was also observed: Path curvature was more pronounced in S-endH (0.058) than in S-begE (0.049), $F(1, 4) = 29.3, p < .01$. This is consistent with the idea that movement was initially directed toward the same location before diverging during the course of the movement, in response to the updating of the target location at the end of the saccadic shift. No statistical interaction was observed for the movement curvature between the experimental factors, $F(6, 72) = 0.3, p > .90$, indicating that the effect of target eccentricity on this parameter was similar for both conditions.

Longitudinal analyses were performed on the instantaneous movement direction (measured with respect to the x -axis) to determine the instant of path divergence among the experimental conditions. These analyses showed that the movement was originally initiated in the same direction for the two experimental conditions. For instance, 120 ms after hand movement onset, the movement direction was equal to 64.9° and 64.7° , on average, for S-endH and S-begE, respectively, $F(1, 4) = 0.1, p > .70$. The first statistically significant effect of the condition factor on movement direction was observed 270 ms after movement onset, $F(1, 4) = 9.1, p < .04$. At this time, a clockwise rotation of the movement direction was observed in S-endH (50.6°) with respect to S-begE (51.4°). No difference in the time of divergence was observed for the different target eccentricities, as shown by the absence of a Target \times Condition interaction, $F(6, 24) = 0.5, p > .80$.

In light of the previous results, one may wonder whether path divergences occurred before or after target refixation (i.e., whether fixation following the corrective saccade represented the critical signal path updating). To address this possibility, we compared the time to target refixation (end of the corrective saccade) with the instant of path divergence. Different results were observed depending on the target eccentricity (due to the fact that saccadic duration increased with the saccadic eccentricity). For the closest target (T1), refixation was observed 50 ms before the instant of path correction. For the furthest target (T7), refixation was observed 12 ms after the instant of path correction. This suggests that refixation was not the critical signal allowing path corrections in the S-endH condition. We return to this point in the discussion.

Hand Velocity Profiles: Corrected and Uncorrected Velocity Profiles Exhibit Similar Bell Shapes

As shown in Figure 13, on the basis of representative trials, path corrections did not notably alter the shape of the hand velocity profiles. In the two experimental conditions, these profiles were

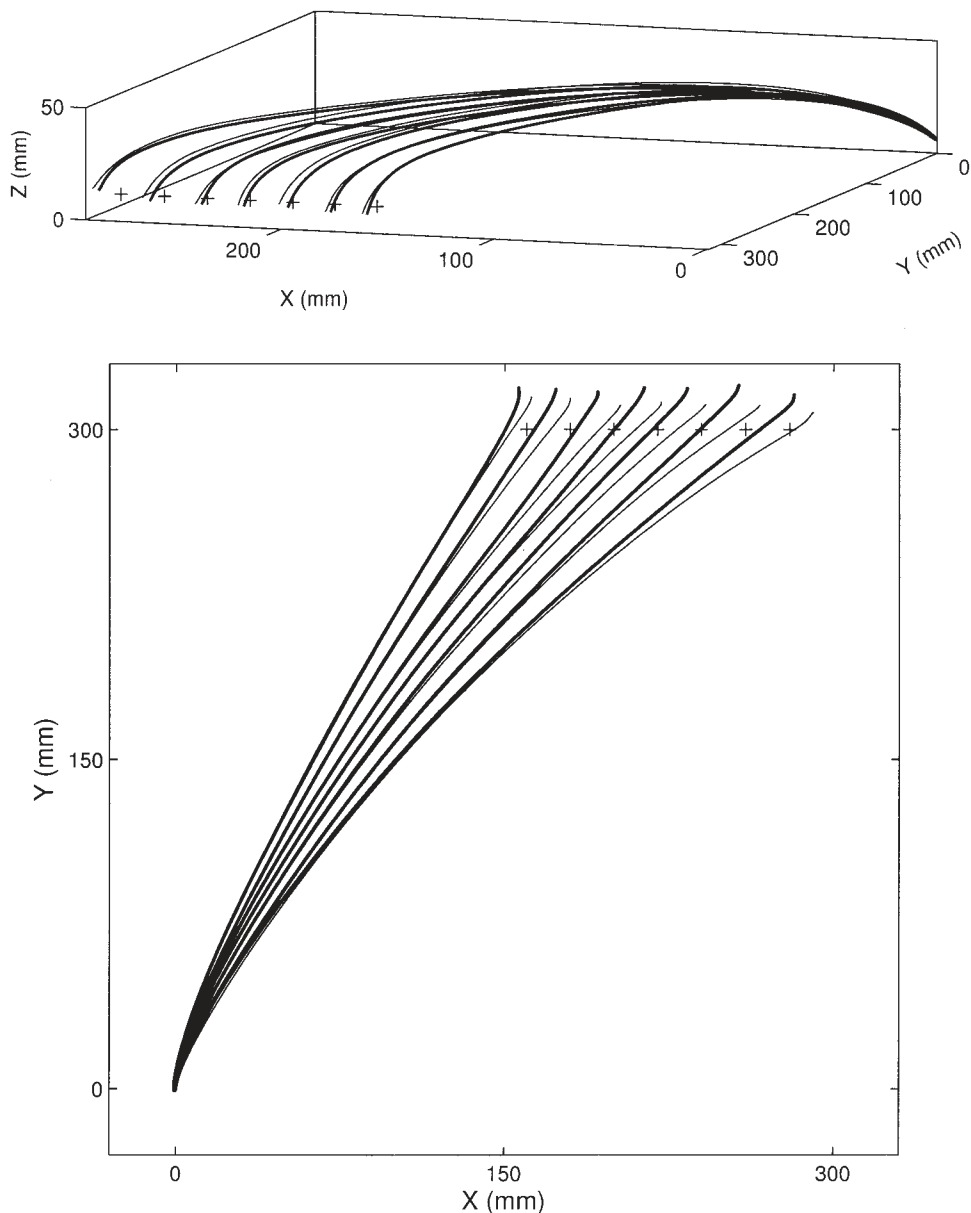


Figure 11. Three-dimensional (top panel) and horizontal (bottom panel) mean hand paths averaged across all subjects for the two experimental conditions. + = target; thick lines = S-begE = saccade permitted, with target on until beginning of eye movement; thin lines = S-endH = saccade permitted, with target on until end of hand movement.

single peaked and roughly bell shaped, although asymmetric. Quantitative analyses indicated that the symmetry index did not vary as a function of the condition factor (.34 vs. .35; main effect and interaction, $ps > .30$). An absence of a significant effect of the condition factor was also observed when the global shape index was considered (2.2 vs. 2.3; main effect and interaction, $ps > .10$). This conclusion is consistent with the results of the shape analysis. Indeed, the similarity index computed by comparing each normalized velocity profile to a reference curve (see the *Method* section of Experiment 1) was not influenced by the ability to update the target location at the end of the saccadic shift (main effect and interaction, $ps > .20$). As in the first experiment, neither these

results nor the observations provided in the sections above were modified when the few movements exhibiting discrete corrections during the deceleration phase (<5%) were removed. Thus, it does not seem that discrete corrections during deceleration can account for the path corrections that occur when the target location is updated at the end of the saccadic shift.

Discussion

In summary, this second experiment shows that the ability to update the target location influences both the path curvature and the accuracy of unconstrained reaching movements. Chronometric

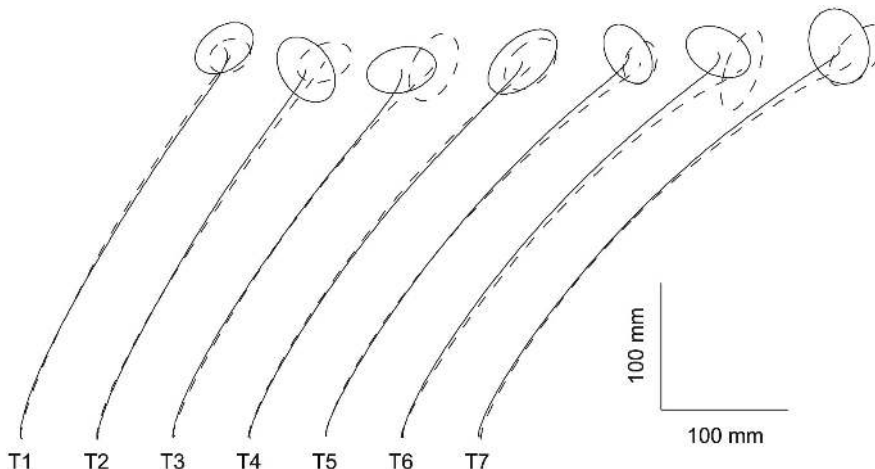


Figure 12. Mean hand path and 95% end-point confidence ellipses for 1 subject and for all target locations (T1-T7). Solid lines = S-begE = saccade permitted, with target on until beginning of eye movement; dashed lines = S-endH = saccade permitted, with target on until end of hand movement.

and kinematic analyses provide strong evidence that this influence takes the form of a smooth feedback-related modulation of the ongoing command. In short, our results show that (a) the hand starts moving either just after or slightly before completion of the

first saccade, (b) the initial characteristics of the movements are identical in all conditions, (c) the hand paths start diverging 270 ms after hand movement onset, and (d) the global shape of the velocity profiles remains similar irrespective of the occurrence of significant path corrections.

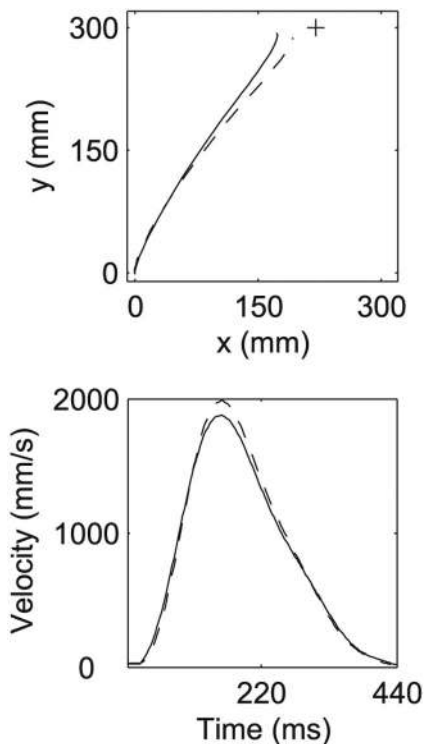


Figure 13. Representative individual trials recorded for the middle target (T4) in the two experimental conditions. Top: Hand paths, with the cross representing the target location. Bottom: Corresponding velocity profiles aligned on movement onset. As can be seen, the movement velocities present very similar shapes in the two experimental conditions. Solid lines = S-begE = saccade permitted, with target on until beginning of eye movement; dashed lines = S-endH = saccade permitted, with target on until end of hand movement.

The Ability to Update the Location of the Target at the End of the Saccade Decreases Systematic and Variable End-Point Errors

In this second experiment, the effect of updating the target location on movement accuracy was smaller than in the first experiment. The existence of substantial differences in the experimental protocols used in the first and second studies is the most likely origin of this quantitative discrepancy. At a qualitative level, we found in this second study that only the final movement direction was affected when updating of the target location was allowed at the end of the saccadic shift. This observation reinforces the conclusion of the first experiment that target eccentricity is underestimated in the peripheral visual field, whereas target elevation is correctly measured. As in the first experiment, however, the absence of an effect of the experimental condition on the errors observed along the axis orthogonal to the saccadic displacement could have been favored by the frontoparallel organization of the target array.

Regarding variable errors, we found, as in the first experiment, that end-point dispersion was significantly reduced when updating of the target location was allowed at the end of the saccadic shift. In contrast to the results of the first experiment, however, we did not find this reduction to be restricted to the directional component of the movement. There is no irrefutable explanation for this discrepancy. However, a plausible hypothesis might be that different types of movements (constrained vs. unconstrained) were studied in the first and second studies. Abundant evidence suggests that the motor system processes movement direction and movement amplitude independently for planar responses (see Desmurget et al., 1998, for a review). This independence causes the distribution of the variable errors to be typically elongated in the

hand–target vector direction, as observed in our first study (Desmurget, Jordan, et al., 1997; Desmurget et al., 1999, 2003; Gordon et al., 1994; Messier & Kalaska, 1999; Vindras & Viviani, 1998). For unconstrained movements, the amplitude–direction hypothesis has received far less support (Atkeson & Hollerbach, 1985; Desmurget, Jordan, et al., 1997; Desmurget et al., 1999; Osu et al., 1997; Rosenbaum et al., 1995; Soechting & Lacquaniti, 1981; see Desmurget et al., 1998, for a review). In this case, and as observed in our second experiment, end-point ellipses are not always robustly elongated in the hand–target vector direction. Some studies have reported quasi-circular ellipses for unrestrained reaching movements comparable to those of our second study (Desmurget, Jordan, et al., 1997; Desmurget et al., 1999). Other work has described a pattern of errors consistent with a shoulder-centered frame of reference (e.g., Flanders et al., 1992) and has argued that errors are due to approximations in the sensorimotor transformation from target position to desired arm posture. It has also been claimed that—at least in the case of memorized targets—the distribution of errors originates from the representation of the target within a frame of reference centered on the eye (McIntyre, Stratta, & Lacquaniti, 1997, 1998).

To explain why the decrease in end-point variability was restricted to the direction variability in our first experiment, we have suggested that the variability in planning (or controlling) the movement direction was smaller than the variability in planning (or controlling) the movement extent. In this case, a homogeneous decrease of the variability in estimating the target position is expected to have a larger impact on movement direction than on movement extent, thus leading to a modification of the shape of the end-point confidence ellipse. Now, if movement direction and movement amplitude are not dissociated during movement planning, as has been proposed to be the case for unconstrained movements, this effect no longer holds, and a homogeneous decrease of the end-point variability is expected to occur.

Feedback Mechanisms Influence Hand Path Curvature

Another important result of this second study concerns hand path curvature. This variable has often been considered a critical insight into how visually directed movements are planned and controlled. For many authors, variations of movement curvature have been a cornerstone in the establishment of their theories. For instance, in a remarkable modeling study, Flash (1987) presented evidence that movements were planned to follow a straight line path but that uncompensated biomechanical forces caused the actual trajectory to deviate from the desired path. Building on this work, several authors presented contradictory arguments suggesting that variations in path curvature did not simply reflect the existence of uncompensated biomechanical forces but also the process of movement planning (Desmurget et al., 1999; Haggard & Richardson, 1996; Harris & Wolpert, 1998; Nakano et al., 1999; Osu et al., 1997; Rosenbaum et al., 1995; Soechting et al., 1995; Uno et al., 1989; Wolpert et al., 1994). Although the present experiment does not challenge this assumption, it shows that movement curvature is also influenced strongly by feedback mechanisms. This result reinforces the conclusion raised elsewhere (Desmurget et al., 1998) that movement curvature represents a multifactorial parameter that reflects the interaction of different, independent factors such as the pattern of movement planning (Harris & Wolpert, 1998; Uno et al., 1989), the action of uncom-

pensated biomechanical forces (Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992; Flash, 1987), the existence of distortions in the perception of straightness (Foley, 1980; Wolpert et al., 1994), and the influence of online adjustments (present study).

Perifoveal Capture of the Target at the End of the Primary Saccade Drives Feedback Corrections

A last interesting result of this second study concerns the issue of target refixation. Our data indicate path corrections can be initiated before actual completion of the corrective saccade (i.e., of actual refixation). This suggests that perifoveal capture of the target at the end of the first saccade might be the relevant signal allowing updating of the target location and thus implementation of a motor correction. This hypothesis is all the more plausible given that the time of path divergence (270 ms) is likely to have been overestimated in the present study. Indeed, temporal averaging of individual hand paths is a noisy procedure because of variations in movement paths and movement durations. When the signal-to-noise ratio is improved, that is, when the path divergences are more sizable, as is the case in subliminal double-step experiments, path divergences are generally detected earlier. For instance, Prablanc and Martin identified significant path differences 150 ms after hand movement onset (Prablanc & Martin, 1992). In agreement with the idea that the perifoveal capture of the target at the end of the primary saccadic response represents the critical signal for path corrections, subliminal double-step studies have repeatedly shown that hand path adjustments can occur before the completion and even the initiation of a corrective saccade (Desmurget et al., 2004; Prablanc & Martin, 1992; Sarlegna et al., 2003).

Conclusive Remarks

Some ideas seem indestructible, even in the face of facts. During recent decades, subliminal double-step experiments (in which the location of the target is modified during gaze shift) have provided converging evidence that (a) fast reaching movements are influenced by feedback control, (b) feedback loops can operate in the absence of visual input of the limb, on the basis of the proprioceptive and/or efferent signals, (c) hand path corrections are not always associated with the generation of discrete submovements, and (d) the combination of both a roughly straight path and a single-peaked, approximately bell-shaped velocity profile is not sufficient to assert that a movement is ballistic (for reviews, see Desmurget & Grafton, 2000, 2003). Despite these observations, it is still common in modeling, behavioral, and imaging studies to evaluate movement characteristics under the assumption that movements exhibiting roughly straight hand paths and bell-shaped velocity profiles are determined by central planning processes (see the introduction).

We have no definitive answer as to why these results from double-step experiments are so widely overlooked. A first possibility might be that feedback loops are often associated with vision. As shown in most point-to-point reaching experiments, feedback loops depending on vision of the arm operate mainly toward the end of the trajectory through the generation of discrete corrective submovements (for reviews, see Carlton, 1992; Desmurget & Grafton, 2003; Jeannerod, 1988). The persistent idea that discontinuities are a necessary correlate of hand path adjustments

may originate from results such as these. This association may have been further reinforced by studies in which a pattern of late discrete corrections was identified for movements performed without vision of the limb (e.g., Elliott et al., 1991; Meyer et al., 1988). A second (non-exclusive) possibility explaining why double-step studies are so widely overlooked might lie in the belief, expressed on different occasions to some authors of this article, that both subliminal double-step studies and behavioral studies involving visual distortions within a virtual environment (Saunders & Knill, 2004) represent artificial paradigms whose results are not directly relevant to describe and understand the organization of normal reaching movements. As claimed by an anonymous colleague at a recent congress, “this is interesting, but my pen usually doesn’t jump when I try to grasp it and neither does the button of the elevator” (personal communication, May 2002). This is true. However, the argument falls short if one considers that the exact location of the target has to be updated at the end of the saccade whether or not the target jumps. In this context, double-step trials appear to be functionally identical to single-step trials such as those examined in the current study. The results of the current study reinforce the view that single-step and double-step movements are identical with respect to the importance of updating the estimation of target location and the prevalence of feedback control. The double-step paradigm merely increases an error that is already present in the system by changing the target location during gaze shift (for discussions, see Desmurget & Grafton, 2000, 2003).

In summary, the present study indicates that the simple point-to-point movements classically studied in the literature cannot be considered ballistic even if they present a roughly straight path and a single-peaked, approximately bell-shaped velocity profile. Error correction mechanisms are in operation, even during simple point-to-point movements. A main source of error is related to the fact that the initial motor command sent to the arm is issued on the basis of an inaccurate estimation of the target location by the peripheral retina. Other types of errors (that are not precisely identified in the current study) are also corrected, as shown by our inability to consistently predict the final variability in movement amplitude on the basis of the early variability in movement acceleration, even when errors in target localization were eliminated.

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