

Seeing the hand while reaching speeds up on-line responses to a sudden change in target position

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Goal-directed movements are executed under the permanent supervision of the central nervous system, which continuously processes sensory afferents and triggers on-line corrections if movement accuracy seems to be compromised. For arm reaching movements, visual information about the hand plays an important role in this supervision, notably improving reaching accuracy. Here, we tested whether visual feedback of the hand affects the latency of on-line responses to an external perturbation when reaching for a visual target. Two types of perturbation were used: visual perturbation consisted in changing the spatial location of the target and kinesthetic perturbation in applying a force step to the reaching arm. For both types of perturbation, the hand trajectory and the electromyographic (EMG) activity of shoulder muscles were analysed to assess whether visual feedback of the hand speeds up on-line corrections. Without visual feedback of the hand, on-line responses to visual perturbation exhibited the longest latency. This latency was reduced by about 10% when visual feedback of the hand was provided. On the other hand, the latency of on-line responses to kinesthetic perturbation was independent of the availability of visual feedback of the hand. In a control experiment, we tested the effect of visual feedback of the hand on visual and kinesthetic two-choice reaction times – for which coordinate transformation is not critical. Two-choice reaction times were never facilitated by visual feedback of the hand. Taken together, our results suggest that visual feedback of the hand speeds up on-line corrections when the position of the visual target with respect to the body must be re-computed during movement execution. This facilitation probably results from the possibility to map hand- and target-related information in a common visual reference frame.

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When reaching for a target object, the afferent signals provided by different sensory channels are continuously processed to supervise the ongoing movement (Wolpert *et al.* 1995; Desmurget & Grafton, 2000). If a discrepancy is detected between the predicted end-point of the movement and the target location – e.g. caused by motor errors or unexpected perturbations – the arm trajectory is modulated on-line to compensate for the detected error and preserve reaching accuracy. For instance, visually detected changes of the target location occurring during movement execution (Soechting & Lacquaniti, 1983; Goodale *et al.* 1986; Prablanc & Martin, 1992; Day & Lyon, 2000; Day & Brown, 2001; Johnson *et al.* 2002; Sarlegna *et al.* 2003) or a load perturbation unexpectedly applied to the reaching arm (Vince, 1948; Crago *et al.* 1976; Cordo, 1990; Smeets *et al.* 1990) can trigger on-line corrections of the hand trajectory. Visual feedback of the

hand position plays an important role in this control. In particular, it increases the reaching accuracy (Woodworth, 1899; Bard *et al.* 1985; Spijkers & Lochner, 1994; Spijkers & Spellerberg, 1995; Proteau *et al.* 2000). Also, when the mapping between the viewed and the actual hand position is altered, the hand trajectory is modulated according to the viewed position (Sarlegna *et al.* 2003, 2004; Saunders & Knill, 2003, 2004; Sober & Sabes, 2003, 2005; Sarlegna & Sainburg, 2007). Here, we tested whether visual feedback of the hand affects the latency of on-line responses to an external perturbation when reaching for a visual target.

In most reaching situations, both kinesthetic and visual information about the hand are used to control the movement (Sarlegna *et al.* 2003). However, visual and kinesthetic signals can also be processed separately to control reaching movements. Indeed, accurate reaching movements can be performed without visual feedback

of the hand (Pelisson *et al.* 1986; Prablanc & Martin, 1992; Blouin *et al.* 1993; Sarlegna *et al.* 2006) as well as in the absence of proprioception (Blouin *et al.* 1993). In line with this, several studies suggested that visual and kinesthetic afferents might underlie two 'parallel' modes of controlling reaching movements: a kinematic mode for the reaching trajectory – mainly relying on visual information, and a dynamic mode for muscle forces – mainly relying on kinesthetic information (Krakauer *et al.* 1999). For instance, visual feedback of the hand is not necessary for learning novel dynamics (DiZio & Lackner, 2000; Tong *et al.* 2002; Osu *et al.* 2004; Scheidt *et al.* 2005; Franklin *et al.* 2007). Along the same line, kinematic and dynamic internal models can be learned independently from each other, based on errors computed in different coordinate frames (e.g. visual and kinesthetic reference frames, respectively; Krakauer *et al.* 1999). Yet, if two such modes of control are used by the central nervous system, then the availability of visual information about the hand should affect the mode in which the movement is controlled. Specifically, when reaching for a visual target with visual feedback of the hand, the relative positions of the hand and target can be computed in a unique, visual coordinate frame. On the other hand, when visual feedback of the hand is not available, kinesthetic signals about the hand/arm and visual signals about the target have to be mapped into a common coordinate frame. Such mapping between coordinates might have processing costs, in which case on-line responses to a detected reaching error should take place with a delay when no visual information about the hand is available. In line with this, we tested here whether the latency of on-line responses to external perturbation depends on the presence of visual feedback of the hand.

On-line corrections take place with a latency with respect to the perturbation because of the time required to process the afferent signals and trigger the appropriate response. Therefore, the latency of on-line responses can be used as a behavioural indicator of the underlying sensorimotor processes. In particular, given that the mechanical constraints of the motor output are identical, different response latencies for two types of stimulus would suggest that the sensory information is processed differently for the two stimuli. We used a protocol in which reaching movements for a visual target were perturbed, and we measured both the first observable corrections of the hand trajectory and the electromyographic (EMG) latency of the responses to the perturbation. Trajectory corrections and EMG latencies were compared with and without visual feedback of the hand. As mentioned above, we reasoned that if the mode of control of reaching movements is affected by visual information about the hand, then the responses to perturbation should occur faster with visual feedback of the hand. We used two different types of perturbation: a

pure visual perturbation and a kinesthetic perturbation. This allowed us to test whether visual feedback of the hand similarly affects the latency of the corrections, irrespective of the modality in which the perturbation is detected. The visual perturbation was a target jump, i.e. a sudden change of the spatial location of the target, whereas the kinesthetic perturbation consisted of a force step applied to the reaching hand. The two types of perturbation occurred at identical times during movement execution, and required comparable on-line corrections of the hand trajectory. Both types of perturbation were tested with and without visual feedback of the hand.

In addition to the main experiment, we conducted a control experiment in which we measured the latencies of two-choice reaction times (see online Supplemental material). As in the main experiment, we used visual and kinesthetic stimuli and tested whether the response latencies were affected by the visual feedback of the hand. However, whereas in the main experiment the perturbation occurred while the subject was performing reaching movements, in the control experiment the stimuli occurred while the subject was holding the hand stationary in space. So the main difference between the two experiments was the task in which the subject was engaged at the time of the perturbation/stimulation. The control experiment was aimed at contrasting the role of visual information about the hand in motor control with its role in a standard reaction time task. In particular, because coordinate frame transformations are not critical in a two-choice reaction time task, we expected that the visual feedback of the hand would not affect the latency of the responses in the control experiment.

Methods

Participants

Eleven right-handed subjects (age 20–37, 5 female) completed the full set of conditions of the experiment. None of them had a history of sensorimotor disorder, and all had normal or corrected-to-normal vision and good stereo vision. All participants gave their informed consent before taking part in the experiment, which was approved by the Ethics Committee of the University Clinic of Tübingen, and conformed with the Declaration of Helsinki.

Experimental set-up

The experimental set-up is shown in Fig. 1. The subjects were seated with their head resting on a chin and forehead rest. In their right hand, they held a vertical handle mounted on a haptic device with four degrees of freedom (DekiFeD, Technische Universität München, München, Germany, Buss & Schmidt, 1999). The haptic

device recorded the subject's hand position and rendered the haptic scene, which was restricted to a 37 cm \times 50 cm horizontal plane at the height of the subject's navel. The visual scene was rendered on a CRT monitor mounted with the screen tilted downwards, and the subjects viewed its reflection binocularly in an opaque mirror through liquid-crystal shutter glasses (Stereographics/REAL D, Beverly Hills, CA, USA). The 3D visual and haptic scenes matched spatially. The visual scene consisted of three spheres of 5 mm radius. Two spheres were magenta and represented the starting position for the reaching movements and the target to reach, respectively. The third sphere was red and provided feedback of the hand position – i.e. position of the top of the handle.

EMG recordings

EMG activity of the right pectoralis major (arm adductor) and posterior deltoid (arm abductor) muscles were recorded using surface cup-electrodes of 10 mm diameter. Two pairs of electrodes were placed near the middle third of the muscles after cleaning the skin with alcohol, along a line parallel to the muscle fibre orientation (Cram, 2003; Brindle *et al.* 2006). A ground electrode was attached to the subject's right wrist. These electrodes were connected to an amplifier (Psylab EEG8, Contact Precision Instruments Inc., Boston, MA, USA) and afterwards via an AD converter (5 kHz sampling rate, DAQ2205, Adlink Technology Inc., Taiwan) to a PC. The signal was band-pass filtered from 3 Hz to 400 Hz from the amplifier. A custom-made MATLAB (The MathWorks,

Natick, MA, USA) program on the PC saved the potentials from both muscles separately, from 300 ms before until 1000 ms after a trigger indicating the perturbation.

Procedure

At the beginning of each trial, the starting position and visual feedback of the hand position appeared simultaneously. The starting position was randomly jittered in a 2 cm \times 2 cm area located 10 cm in front of the subject about body midline. After the visual feedback of the hand position had been maintained in the starting position for about 1 s, the target appeared and the starting position disappeared. The subject's task was to reach for the target as quickly and precisely as possible. For the trials without visual feedback of the hand, the red sphere representing the top of the handle disappeared as soon as the target appeared. The target was located 20 cm from the starting position, either straight ahead or 30 deg on either side of body midline. For some trials, the reaching movement was perturbed, forcing the subject to modify the hand trajectory on-line. Two types of perturbation were used: the visual perturbation consisted of suddenly displacing the target by 7.5 deg, either rightward or leftward with respect to its original location (Fig. 2A). The kinesthetic perturbation was a force of 10 N applied perpendicularly to the reaching direction over a path length of 10 cm (Fig. 2B). The force could come either from the right or from the left. The perturbation occurred either 1 or 5 cm after the starting point of the reaching movement, for the rest of the paper referred to as early and late perturbation, respectively. The time at which the velocity of the hand

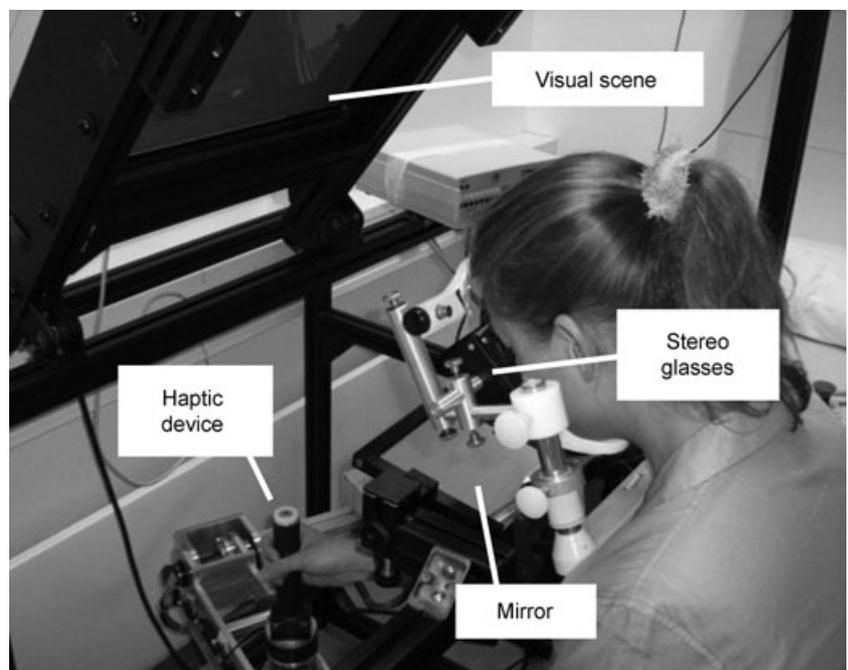


Figure 1
Experimental set-up.

dropped below 1 cm s^{-1} was defined as the end of the trial. At that time, the visual scene disappeared.

Blocks and duration

Each subject first conducted a training block of 96 trials to familiarize himself with the set-up and the perturbations. Then, the four blocks of the main experiment (192 trials each) and the block of the control experiment (64 trials, see Supplemental material) were performed. Half of the subjects performed the main experiment first whereas the other half started with the control experiment. Each experimental block consisted of two repetitions of the full permutation of all independent variables: two perturbation types (visual; kinesthetic), two feedback types (visual feedback of the hand; no visual feedback), two perturbation onsets (1 cm, early; 5 cm, late), three target locations (30 deg to the left; 30 deg to the right, or straight to the middle) and two perturbation directions (right; left). An equal number of unperturbed trials was also performed, resulting in a 50% chance for a perturbation to occur. In each block, the order of presentation of the trials was fully randomized. Mixing all conditions in each block prevented any predictability or anticipation concerning the perturbation of the reaching movements. Two seconds separated each trial from the next one. Overall, each subject performed 928 trials and the experiment lasted between 90 and 120 min, with a 3 min pause every 20–25 min.

Measured variables

We measured the reaching accuracy and the latency of on-line responses to perturbations. The reaching accuracy was used as an indicator of the functional efficiency of the corrections. However, the latency constituted our main focus of interest since we wanted to determine whether visual feedback of the hand speeds up the

occurrence of on-line responses. The latency of the responses was assessed measuring both the kinematic of the hand trajectory and the neuro-muscular activity (EMG latency) correlated to the reaching movements. All reported latencies, whether kinematic or EMG, are relative to perturbation onset.

Reaching accuracy

The onset and the end of the movement were defined as the first time the velocity of the hand raised above and dropped below 2 cm s^{-1} , respectively. For unperturbed trials, the reaching accuracy was defined as the angle in degrees between the top of the handle at the end of the movement and the reached target. For perturbed trials, the reaching accuracy was the reaching error in degrees with respect to the unperturbed reaching movements for the corresponding target.

Kinematic latency of on-line corrections

We assessed the first correction-specific changes of the hand trajectory. For that, we measured the first deviations of the hand path ('PATH') as well as the first changes of hand velocity ('VEL'). We focused on the component of the reaching trajectory perpendicular to the vector between the starting position of the hand and the initial position of the target (illustrated in Figs S1 and S2 of the Supplemental material).

For each subject and condition, the PATH latencies were defined as the first time the mean trajectory reached a fixed threshold. Before that, for each condition, the mean of the unperturbed trials was subtracted from each trial to circumvent constant reaching biases. For visual perturbation, the threshold was one quarter of the way to the displaced target. For kinesthetic perturbation, the threshold was one quarter of the way from the maximum displacement until the end of the movement.

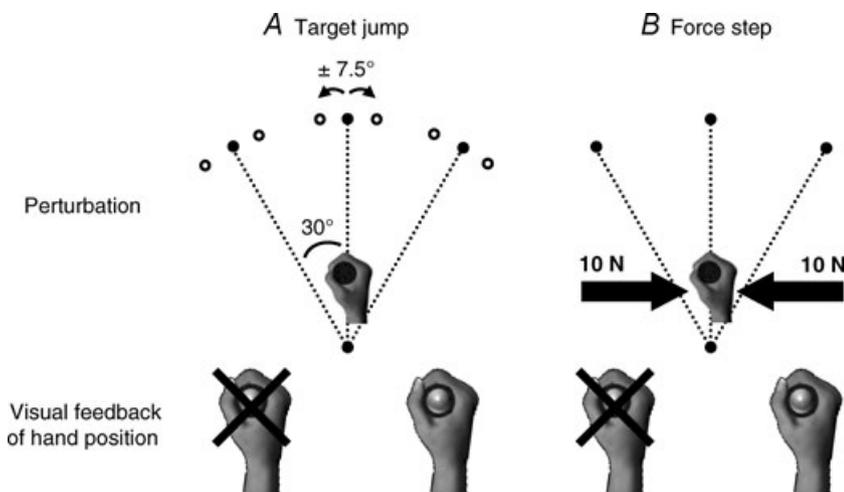


Figure 2. Experimental conditions

Two types of reaching perturbation were used: A, displacement of the visual target, and B, force step applied to the reaching arm. For both types of perturbation, half of the trials were performed with visual feedback of the hand position and the other half without.

This threshold was chosen to identify hand deviation as early as possible. Some studies (Day & Lyon, 2000; Day & Brown, 2001) used measurements more comparable to a 10% threshold. However, in our study, a 10% threshold yielded in many invalid onset times because of the initial variability of the data.

Concerning VEL latencies, the first changes of hand velocity were computed using half the maximum velocity as threshold for visual perturbation, and half the difference between maximum and minimum velocity as threshold for kinesthetic perturbation. These thresholds were chosen because lower thresholds (e.g. a quarter or 10%) provided more variable data and many invalid onset times.

To limit the dependency of the results on the threshold values, PATH and VEL latencies were also determined with two other fixed thresholds as well as using the unperturbed trials as baseline. More details about these additional measurements are provided in the Supplemental material.

EMG latency of on-line corrections

We assessed the first correction-specific changes of EMG activity (i.e. first excitatory bursts). We focused on the shoulder muscles agonistic to the corrective movement, namely the posterior deltoid for trials in which a rightward correction (arm abduction) was required, and the pectoralis major for trials in which a leftward correction (arm adduction) was required. We chose these two muscles because d'Avella *et al.* (2006) showed that they are involved at an early stage in the muscle synergies producing medial and lateral movements of the arm when reaching. We did not measure the activation of elbow muscles since, for on-line responses to both visual and

kinesthetic perturbation, the EMG activation of shoulder and elbow muscles is similar (Soechting & Lacquaniti, 1983; Smeets *et al.* 1990). Also, we did not measure the latency of inhibition of the antagonistic muscle because early inhibitions were very difficult to detect.

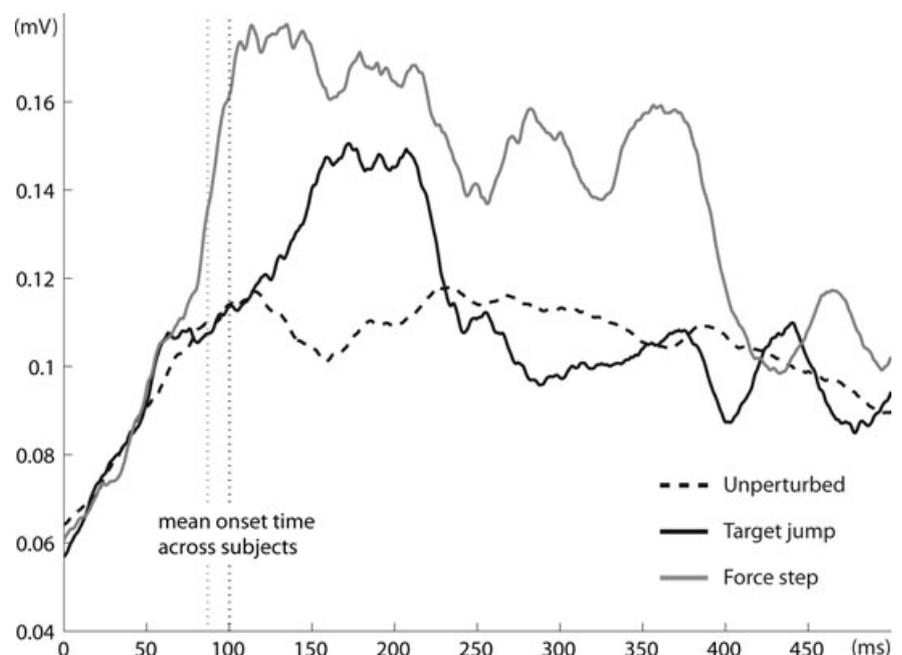
For each EMG trace, the AC component of the signal was rectified and then smoothed using a rectangular moving window of 25 ms to reflect the low pass characteristics of muscle (Hammond, 1960; Eklund *et al.* 1982). The EMG latencies were determined using the mean activation of unperturbed trials as baseline (Fig. 3 shows some exemplary EMG traces). To define correction onset, the EMG trace of the perturbed trials had to stay for 25 ms above the threshold which was set to 110% of the baseline. This procedure resulted in a detection rate of 64.7% and 71.4% for visual and kinesthetic perturbation, respectively.

To avoid a dependency of the results on the threshold values, the data were also analysed with a threshold set at 120% of the baseline. Moreover, in order to limit the dependency of the results on the method chosen, we used an additional and independent EMG measurement to assess the latency of the responses. More details about these additional thresholds and measurements can be found in the Supplemental material.

Data analysis and statistics

Reported values are mean \pm standard error unless stated otherwise. All statistical tests were conducted using analyses of variance (ANOVA). For all measurements, there were no significant interactions between our main variable of interest, i.e. visual feedback of the hand, and target location or perturbation direction.

Figure 3. Group EMG traces of the posterior deltoid muscle for one condition with visual and kinesthetic perturbation, and their corresponding unperturbed trials (target to the left, correction to the right, early onset, with visual feedback of hand position) Time point 0 is the onset time of the perturbation. The dashed lines indicate the mean response latency for these conditions.



Therefore, we pooled the data over target location and perturbation direction. This resulted in $2 \times 2 \times 2$ [type of perturbation (visual, kinesthetic) \times visual feedback of the hand position (without, with) \times onset of perturbation (early, late)] repeated-measures ANOVAs, unless stated otherwise. Also, pre-planned comparisons between corresponding conditions with and without visual feedback about the hand were systematically conducted. Corrections for multiple comparisons were conducted with Newman–Keuls tests for the ANOVAs, or Bonferroni corrected paired t tests ($P < 0.05$) when necessary.

Results

Movement time and time of perturbation onset

Movement times with the two types of perturbation were not significantly different (797.9 ± 38.5 and 809.3 ± 32.1 ms for visual and kinesthetic perturbation, respectively) but were both significantly longer than unperturbed reaching movements (665.2 ± 35.6 ms, $P < 0.001$). Early and late perturbations occurred on average 78.0 ± 22.4 and 180.3 ± 40.2 ms after movement onset, respectively. From perturbation to maximum velocity, 170.8 ± 50.4 ms elapsed for early perturbations and 68.2 ± 44.2 ms for late perturbations. From

perturbation to maximum acceleration, 143.4 ± 64.5 ms elapsed for early perturbations and 40.8 ± 58.5 ms for late perturbations. None of the early perturbations occurred after maximum velocity or maximum acceleration had been reached. As for late perturbations, 2.4% occurred after maximum velocity had been reached (following for 62 ms at most) and 19.2% after maximum acceleration had been reached (following for 215 ms at most). For all those measurements, no difference was found between trials with and without visual feedback of the hand.

Reaching accuracy

When the reaching movements were unperturbed, the subjects reached on average 1.50 ± 0.91 deg to the left of the target without visual feedback of the hand, and 0.17 ± 0.09 deg to the right with feedback (1 deg = 3.5 mm). For perturbed reaching movements, corrections were less complete for kinesthetic vs. visual perturbation ($F_{1,10} = 20.54$; $P < 0.01$), less complete with visual feedback of the hand vs. without ($F_{1,10} = 12.019$; $P < 0.01$), and less complete for late vs. early perturbation ($F_{1,10} = 67.51$; $P < 0.0001$). The comparisons between the corresponding conditions with and without feedback about the hand revealed that for early visual perturbation, the subjects were more accurate when visual feedback of the hand was provided ($P < 0.01$; see Fig. 4).

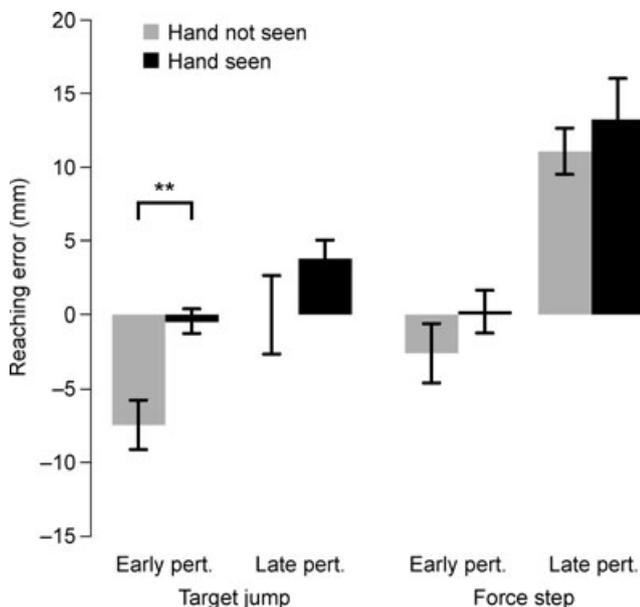


Figure 4. Reaching accuracy with and without visual feedback of the hand, for all combinations between perturbation type and perturbation onset

For early visual perturbation, the trials without visual feedback of the hand exhibited an overcompensation as compared to the trials with visual feedback of the hand. For the late kinesthetic perturbation there was no difference between the trials with and without visual feedback of the hand, the corrections being incomplete in both conditions.

Kinematic latency of on-line corrections

Kinematic analyses did not allow us to compare directly the latency of visual and kinesthetic perturbation. Specifically, whereas for visual perturbation the initial path deviation resulted from the correction, it was produced by the perturbation itself for kinesthetic perturbation. Therefore, our analyses focused on the effect of visual feedback of the hand, which was assessed with Bonferroni corrected paired t tests for each combination between perturbation type and perturbation onset. Both PATH and VEL analyses showed that on-line corrections to early visual perturbation occurred earlier with visual feedback of the hand (see Figs 5 and 6A and B). This pattern of results was identical irrespective of the method of measurement used and the threshold selected (see Supplemental material).

EMG latency of on-line corrections

On-line corrections took place earlier when a force was applied to the arm than when the target position changed ($F_{1,10} = 16.80$; $P < 0.01$). More importantly, the comparisons between corresponding conditions with and without feedback about the hand revealed that visual feedback of the hand sped up the latency of on-line corrections for early visual perturbation (8.9 ± 3.5 ms;

$P < 0.05$). These results are shown in Fig. 7. The same pattern of results was observed with the other method of measurement and with all selected thresholds (see Supplemental material).

Discussion

The main result of the present experiment is that when reaching for a visual target, visual feedback of the hand speeds up the latency of on-line responses to a sudden change of target position. Such latency facilitation was observed only when the change of target position occurred at an early stage of reaching movement execution. Also, visual feedback of the hand did not affect the latency of on-line responses to kinesthetic perturbation. Finally, visual feedback of the hand failed to alter the latency of visual and kinesthetic two-choice reaction times, suggesting that the facilitation observed in the main experiment is specific to on-line responses.

Latency and accuracy of on-line responses in humans

In humans, the reported latencies for on-line responses are very variable, depending on the task and method of measurement used. Kinematic latencies, i.e. the first measured changes of hand path, velocity or acceleration are the most commonly reported for responses to visual perturbations, and they are usually in the range 280–350 ms for path deviations and 190–280 ms for

velocity changes (e.g. Prablanc & Martin, 1992; Johnson *et al.* 2002; Sarlegna *et al.* 2003). The latencies we measured compare well with those values, though slightly longer. Observing such a slight delay in our experiment was to be expected considering the mass/inertia added by the haptic device with which the reaching movements were

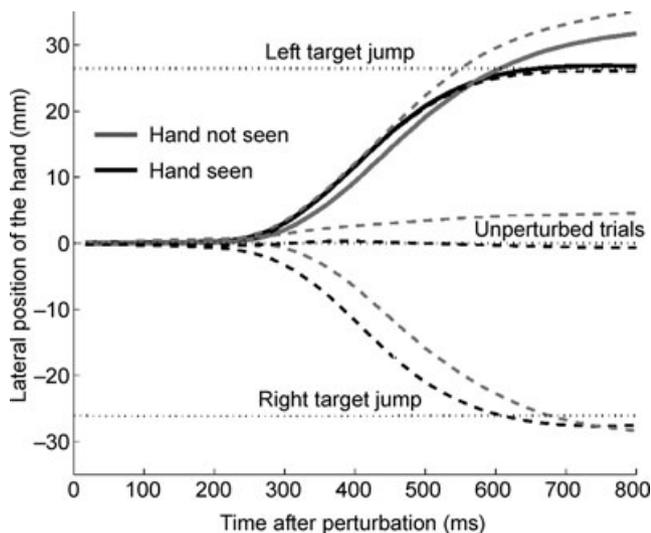


Figure 5. Mean hand trajectories (averaged across subjects and initial target position) for unperturbed reaching movements and ‘early’ target jumps in both directions (left and right) The dashed lines represent the uncorrected trajectories, whereas the continuous lines represent the averaged trajectories for on-line responses to left and right target jumps (unsigned). On-line corrections take place earlier when visual feedback of the hand is provided.

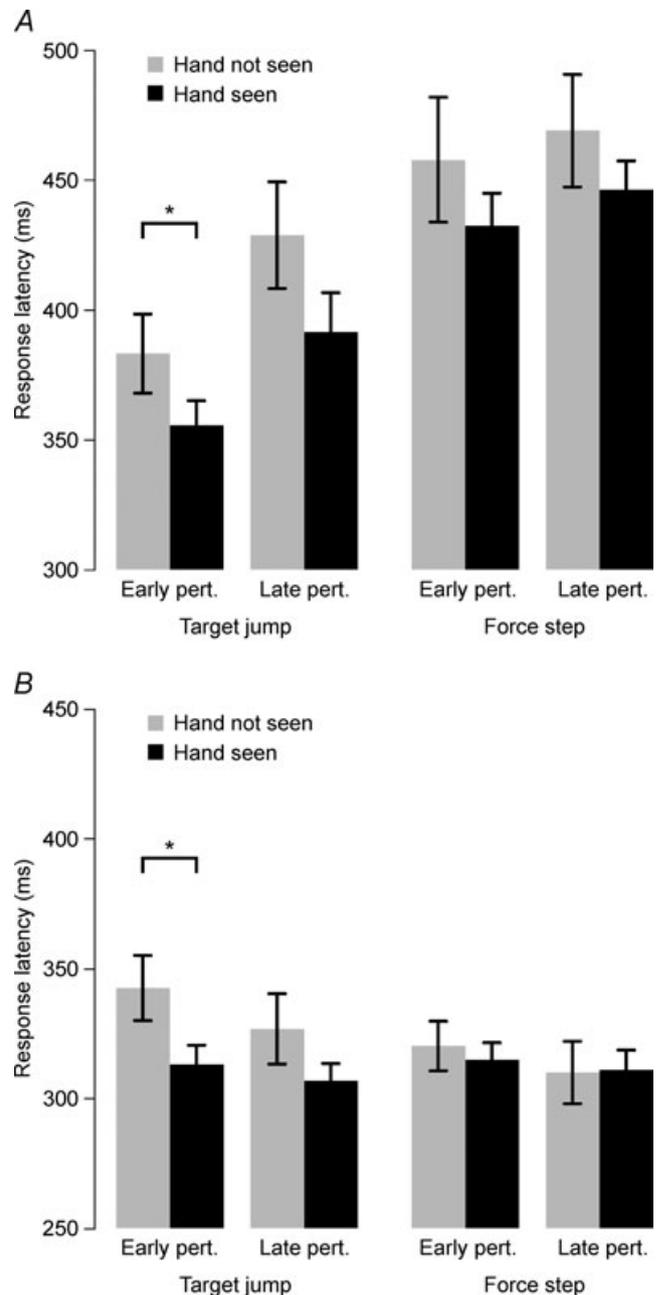


Figure 6. Average onset times of path (A) and velocity deviations (B) based on a fixed threshold with and without visual feedback of the hand, for all combinations between perturbation type and perturbation onset For the responses to early visual perturbation, both measurements show significantly shorter latencies when visual feedback of the hand was provided.

performed. Remarkably, Day & Lyon (2000) measured very short latencies (125–160 ms). This corresponds to what we observed setting the VEL threshold at 10% of the maximum velocity (see Supplemental material). Such a threshold is well suited to detect very early responses but, in our case, it resulted in many invalid onset times. Since we were mostly interested in comparing trials with and without visual feedback of the hand, we opted for a more conservative threshold which allowed more robust comparisons. Concerning responses to kinesthetic perturbation, kinematic latencies are quite variable and little reliable since the first changes of hand path/velocity usually result from the perturbation itself. Therefore, they are difficult to compare between studies when the nature of the kinesthetic perturbation differs. On the other hand, because they constitute a direct measurement of the activity of the muscles producing the movement, EMG recordings constitute a reliable indicator of the latency of responses to kinesthetic perturbation. Also, for both visual and kinesthetic perturbation, EMG recordings allow early detection of on-line responses, which is not possible with kinematic analyses. In humans, the reported EMG latencies for on-line responses to kinesthetic perturbation lie in the range 60–100 ms (Crago *et al.* 1976; Smeets *et al.* 1990). This is similar to what we measured in our experiment. As for responses to visual perturbation, only few studies used EMG measurements to determine their latency. Using a method comparable to ours, Soechting &

Lacquaniti (1983) reported latencies of 110–120 ms, which is similar to what we measured.

Regarding reaching accuracy, we observed mean deviations of less than 3 deg for on-line responses to visual perturbation. This corresponds to the accuracy reported in previous studies using similar perturbations (Cordo, 1990; Prablanc & Martin, 1992; Bard *et al.* 1999; Sarlegna *et al.* 2003). Also, providing visual feedback of the hand increased the reaching accuracy, which is in agreement with previous studies (Woodworth, 1899; Bard *et al.* 1985; Spijkers & Lochner, 1994; Spijkers & Spellerberg, 1995; Proteau *et al.* 2000). The accuracy we measured for on-line responses to kinesthetic perturbation is more difficult to compare with other studies since, to our knowledge, this particular task was used here for the first time. Responses to early perturbations preserved the reaching accuracy, which was similar to that measured for responses to visual perturbation. On the other hand, the corrections taking place with late kinesthetic perturbation were consistently incomplete, and this irrespective of the availability of visual feedback of the hand. In that condition, the force field ended only 5 cm ahead of the target. Our results suggest that this distance is too short for an efficient on-line correction to take place.

Visual feedback of the hand position speeds up on-line responses to early visual perturbation

For both kinematic and EMG measurements, providing visual feedback of the hand during reaching movements significantly shortened the latency of on-line responses to early visual perturbation. Specifically, EMG latencies were about 10 ms shorter and response-specific changes of the hand trajectory were observed about 30 ms earlier with vision of the hand. This consistency in the pattern of response latencies reinforces the hypothesis that the mode of control of reaching movements depended on the availability of visual feedback about the hand. Previous research suggested that the mode in which goal-directed movements are both planned (Sober & Sabes, 2003, 2005; Sarlegna & Sainburg, 2007) and controlled (van Beers *et al.* 1999, 2002) can change as a function of the modality of the target and the nature of the available information about the reaching hand/arm. Our results confirm this hypothesis. In particular, when visual information about the hand position is not available, the kinesthetic signals about the arm position and the visual signals about the target position have to be mapped into a common coordinate frame. On the other hand, when visual information about the hand is available, the relative positions of the hand and target can be computed in a unique, visual coordinate frame. Our results show for the first time that the latter scenario allows faster responses to a change of target position, providing an important insight into the

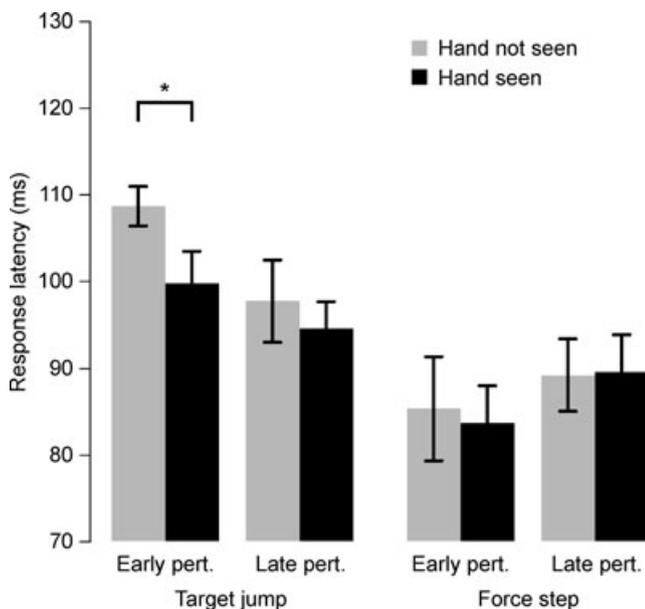


Figure 7. Average EMG response latencies with and without visual feedback of the hand, for all combinations between perturbation type and perturbation onset

For the responses to early visual perturbation, the latency was significantly shorter with visual feedback of the hand.

mechanisms underlying the on-line control of reaching movements.

In contrast to what we observed for early visual perturbation, visual feedback of the hand did not speed up on-line responses to target displacements occurring at a later point of the hand trajectory. This difference can be explained by the temporal relationship between the perturbation and the saccade to the target. In particular, early perturbations occur around the time point of the initial saccade to the target (Prablanc & Martin, 1992). Therefore, the corrective saccade to the displaced target falls into the corrective saccade that is 'pre-packaged' with the initial saccade (Becker & Fuchs, 1969). In this case, there is a stable visual reference frame with respect to the target available very early. Within this visual reference frame, the visual feedback of the hand position is profitable. On the other hand, late perturbations trigger an extra saccade (Becker & Fuchs, 1969), which needs time to initiate and draws attention to the new target. The visual reference frame is shifted and remains unstable for a longer time. In this case, the visual feedback of the hand does not provide any benefit. Also, saccadic suppression might occur during the time-point of correction, preventing the processing of the visual feedback of the hand position.

Most studies using visual perturbation protocols are more comparable to our early perturbation condition as the initial saccade is often used to trigger the perturbation. Our results show that there is an influence of the time point of perturbation that cannot be disregarded. In that respect, investigating the influence of perturbation time point and its interaction with other parameters, such as the availability of sensory information or the modality of perturbation might be an interesting direction for future research.

Visual feedback of the hand position does not affect on-line responses to a force applied to the reaching arm

Visual feedback of the hand did not affect the latency of on-line responses to a force applied to the reaching hand. This result might seem surprising for two reasons. First, since the target was always visual, one could expect visual information about the hand to have the same beneficial influence on the responses to both types of perturbation. Indeed, irrespective of the perturbation type, when visual feedback of the hand is available the relative positions of the hand and target can be coded in a unique visual coordinate frame. In addition, for kinesthetic perturbation, visual information about the hand provided a second sensory cue about the arm deviation. With visual feedback, the subjects could feel their hand position via proprioceptive afferents, and additionally see their hand deviating from the initial trajectory. This additional

sensory cue about the perturbation could have contributed to speed up the responses since previous research has shown facilitation of response times when more sensory channels provide redundant information about the same event (Hershenson, 1962; Morrell, 1968; Bernstein *et al.* 1969; Nickerson, 1973; Gielen *et al.* 1983). This was not the case. The latency of the responses to the force perturbation was identical irrespective of the presence of visual feedback of the hand position.

One notable difference between the two types of perturbation was the spatial relationship between the target and the body. Specifically, as opposed to visual perturbation, kinesthetic perturbation did not alter the spatial position of the target. This implies that the central nervous system did not have to re-compute on-line the target position with respect to the body. The kinesthetic perturbation only required a quick reaction to the force detected by the kinesthetic sensors by sending a motor command to counteract this force. Such a response could be triggered within a 'pure' kinesthetic reference frame (Krakauer *et al.* 1999). In the latter case, no re-mapping between visual and kinesthetic reference frames would be required, which means that no extra processing time would be needed before triggering an on-line response when visual feedback of the hand is not available. In line with this, our results suggest that visual information about the hand reduces the latency of on-line corrections only when the position of the visual target has to be re-coded in a body-centred reference frame during the execution of the reaching movement.

The response facilitation evoked by the visual feedback of the hand is specific to on-line corrections

Although the neural mechanisms underlying the on-line control of reaching movements are not completely known, several experiments suggested that this control relies on automatic, fast feedback loops, that are distinct from the processes involved in 'classic' reaction times. Specifically, on-line corrections of the hand trajectory can occur without awareness (Goodale *et al.* 1986; Prablanc & Martin, 1992; Sarlegna *et al.* 2003) and are difficult to prevent (Day & Lyon, 2000; Pisella *et al.* 2000). Also, the reported latencies of on-line corrections to visual (Carlton, 1981; Soechting & Lacquaniti, 1983; Prablanc & Martin, 1992; Day & Lyon, 2000; Day & Brown, 2001) and proprioceptive perturbations (Vince, 1948; Crago *et al.* 1976; Smeets *et al.* 1990) are much shorter than the latencies of visual (Evarts *et al.* 1981; Day & Brown, 2001; Jaskowski & Sobieralska, 2004) and proprioceptive reaction times (Evarts *et al.* 1981). This is confirmed by our experiment, in which on-line responses to visual and kinesthetic perturbations occurred almost twice as fast as two-choice reaction times to similar stimuli. Finally, a

recent study by Day & Brown (2001) with a split-brain patient suggested that, in contrast to classical reaction times, on-line control of reaching movements might partly be mediated by sub-cortical structures.

In our experiment, visual feedback of the hand facilitated on-line responses to early visual perturbation but did not affect the latency of two-choice reaction times. This constitutes additional evidence that the neural processes underlying on-line responses differ from those underlying mainly preparatory motor processes like classic reaction times (Day & Lyon, 2000). More importantly, it highlights the specificity of the facilitation observed for the on-line responses to early visual perturbation. Since on-line corrections of reaching movements present strong spatial accuracy constraints, coordinate frame transformations constitute a critical issue when performing such corrections. On the other hand, the two-choice reaction time task that we used had very low spatial accuracy constraints. Indeed, the subjects were only instructed to move as fast as possible in the correct direction (i.e. right vs. left). As a consequence, coordinate transformation was critical to perform on-line corrections but not to perform the two-choice reaction time task. In line with this, the absence of a difference in the two-choice reaction time task supports the idea that the facilitation of on-line responses indeed resulted from the availability of sensory information about the hand and the new target in the same coordinate frame.

Neural processing of visual feedback for controlling action

As kinematic measurements also depend on external factors like inertia of the system moved, our discussion will focus here on EMG latencies, which better represent the actual timing of on-line corrections and are therefore more suitable for making inferences about neural processing times. In our experiment, the EMG latency of the responses to early visual perturbation decreased on average from 110 ms when no visual feedback of the hand was available to 100 ms or even less with visual feedback. This constitutes a rough 10% reduction of the gross response latency. In terms of neural processing time actually devoted to sensorimotor integration, however, it represents a much larger reduction. Specifically, the sensorimotor processes underlying the on-line control of reaching movements can be subdivided into three stages. First, the afferent signals are conveyed from the peripheral sensors to the cerebral cortex. Then, the information can be integrated (e.g. in the posterior parietal cortex) and a motor response is selected (e.g. in the supplementary motor areas). This is the stage where coordinate transformation occurs when necessary (Andersen *et al.* 1997; Colby, 1998). Finally, a motor command is sent from the primary motor cortex to

the effectors (muscles). Concerning the sensory processing of visual signals, visual afferents need about 60 ms to reach the cerebral cortex in monkeys (Bullier & Nowak, 1995; Schmolesky *et al.* 1998; Bullier, 2001), whereas the first visual-evoked potentials in humans are usually observed after 70–75 ms (Odom *et al.* 2004). Regarding the time needed for motor commands sent by the primary motor cortex to reach shoulder muscles in humans, transcranial electric and magnetic stimulation studies indicate that it takes about 10–15 ms (Merton & Morton, 1980; Hess *et al.* 1987; Di Lazzaro *et al.* 1998; Bawa *et al.* 2004). Therefore, ‘pure’ visual and motor processes probably add up to about 80 ms. Subtracting these 80 ms from the response latencies we measured, the time actually allotted to sensorimotor integration and motor selection in our experiment decreased from 30 ms without visual feedback of the hand to about 20 ms with feedback. In other words, when the target position changed during movement execution, providing visual feedback of the hand (thereby enabling target- and hand-related information to be mapped in a common visual reference frame) reduced the ‘cortical’ processing time by about 35%. Note that Reynolds & Day (2007) made an analogous but much more conservative estimate of the visuo-motor processing time, evaluating that a minimum of 40 ms is required (rather than 80 ms with our estimate). With such a conservative estimate, the net reduction of cortical processing time allowed by visual feedback of the hand would amount to 15%. Overall, our results suggest that when a coordinate transformation between visual and proprioceptive signals must be performed on-line to re-code the target position in a body-centred reference frame, the neural processing time needed to integrate sensory information and select an appropriate response is notably increased.

Conclusion

Using a task in which reaching movements for a visual target were perturbed by either a change of target location (visual perturbation) or a force applied to the reaching hand (kinesthetic perturbation), we showed that providing visual feedback of the hand reduces the latency of on-line responses to early visual perturbation. On the other hand, when the perturbation was kinesthetic and did not alter the position of the target with respect to the body, the latency of on-line responses remained unaffected by the visual feedback of the hand. A control experiment showed that visual feedback of the hand never speeds up two-choice reaction times, indicating that the facilitation is specific to on-line responses. Taken together, our results suggest that when the position of the target with respect to the body must be re-computed during movement execution, providing visual feedback of the hand speeds up on-line corrections by enabling hand- and target-related

information to be mapped in a common visual reference frame.

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Author contributions

A.R. and J.-P.B. conceived and designed the experiments. A.R. analysed the data and all authors contributed to their interpretation. A.R. and J.-P.B. wrote the article. A.T., A.P. and H.H.B. contributed to the revision of the draft. All authors approved the final version of the article.

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