Title: Rapid online correction is selectively suppressed during movement with a visuomotor transformation

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Abstract

Reaching movements to visual targets are under fast feedback control, which can rapidly correct an ongoing movement for errors. This study investigates how this online correction is affected by the application of a new visuomotor transformation. Thirty-two subjects made planar pointing movements to visual targets. Vision of the arm was prevented and hand position was represented by a cursor displayed in the movement plane. In some trials the target abruptly changed location at the onset of arm movement, which required a rapid correction of movement direction. After performing baseline trials, some subjects were required to adapt to a mirror-image transformation that inverted the visual feedback of their hand position across the body midline, while others were not familiarized with the transformation. Afterwards, subjects’ online correction was tested with target jumps in the presence of the mirror transformation. Results show that after short-term motor adaptation to the mirror transformation there was a selective suppression of the rapid non-mirror correction in the direction of visual target displacement, but no mirror reversal. The suppression occurred within the first few trials after the introduction of the mirror transformation and it was strongest for the movements in which the transformation caused the largest dissociation between the target location and hand movement. Finally, whether or not the short-latency non-mirror correction was suppressed in a given trial, the mirror correction occurred at the same latency as the onset time of voluntary correction in subjects who had not experienced the mirror transformation.
Introduction

Studies of plasticity of human motor control can reveal underlying functional mechanisms and improve our understanding and rehabilitation of movement disorders. Some early studies of plasticity of goal-directed movements used prisms to displace or completely invert visual input to observe the induced sensorimotor adaptation (Harris 1963; Held and Bossom 1961; Held and Schlank 1959; Kohler 1963; Stratton 1897; 1899; von Helmholtz 1925). These studies showed that motor adaptation can be as rapid as minutes when people learn to point to targets viewed through lateral-displacing prisms (Harris 1965; von Helmholtz 1925), or as long as days and weeks when people learn to move around in the world while wearing inverting prisms (Kohler 1963; Stratton 1897). These studies have shown that subjects can apply a new mapping between visual input and voluntary motor output. However, what sensorimotor mechanisms are involved in the learning of this new mapping is still a matter of active study.

During normal reaching movements, motor execution is under control of multiple feedback loops. One such feedback circuit is the so-called “rapid online correction” mechanism. It was first demonstrated by studies that displaced the location of the reach goal shortly before or after the onset of movement and observed robust short-latency corrections of hand trajectory toward the new target location (Cooke and Diggles 1984; Desmurget et al. 1999; Elliott and Allard 1985; Higgins and Angel 1970; Jaeger et al. 1979; Pelisson et al. 1986; Pisella et al. 2000; Prablanc and Martin 1992; Sarlegna et al. 2003, 2004). The online correction mechanism appears to be activated automatically by visuomotor errors during reaching movements, because the onset latency of correction is significantly shorter than normal voluntary movement reaction times (Higgins and Angel 1970; Jaeger et al. 1979; Cooke and Diggles 1984) and because the online correction is evoked by target jumps that are not consciously perceived (Johnson and Haggard 2005; Pelisson et al. 1986; Turrell et al. 1998). Furthermore, Day and Lyon (2000) demonstrated that the online correction mechanism is resistant to cognitive control, such as instructions
to voluntarily respond to target displacements by moving the arm in the direction opposite to the target jump (Day and Lyon 2000). Subjects persisted in making an initial small short-latency non-mirror reach deviation in the spatial direction of the target displacement, followed by a delayed mirror deviation in the opposite direction at about the normal voluntary reaction time after the target displacement.

The Day and Lyon (2000) study demonstrated that short-term experience with an arbitrary mirror transformation is not adequate to alter the mapping between visual input and motor output in the rapid online correction mechanism. However, in that study subjects continued to initiate reaching movements to the spatial location of the visual targets and only applied the mirror transformation to the target displacements. No one has yet looked at what happens when subjects perform reaching movements in an environment in which they are immersed in a visuomotor dissociation. Does the mapping within the rapid online correction mechanism change in parallel with the transformed reach trajectories as subjects adapt to a visuomotor dissociation or are the two processes independent and have different time-courses? Other studies have shown that some reflex pathways are amendable to adaptive modulation. For example, operant conditioning of H-reflex has been demonstrated in animals (Carp et al. 2006; Chen and Wolpaw 1995; Wolpaw 1987; Wolpaw and Herchenroder 1990) and humans (Evatt et al. 1989; Trimble and Koceja 1994; Wolf and Segal 1996). The present study explores the question of plasticity of the online correction mechanism during reaching with a mirror transformation. We addressed this question by having human subjects practice moving a cursor to visual targets with or without a mirror transformation and without target jumps and then assessing whether adaptation to the mirror transformation would generalize to rapid online corrections when target jumps are introduced within a mirror-transformed environment. Furthermore, we investigated the contribution of visually-derived hand position information for plasticity of online control by studying trajectory corrections with and without continuous visual (cursor) feedback of subjects’ hand movements.

**Materials and methods**
Experimental apparatus

The task apparatus consisted of a digitizing tablet to capture hand movement, and a suspended LCD monitor (VX924, ViewSonic Co, Walnut, CA), which was capable of displaying visual stimuli with a minimum delay of 3 ms. Visual targets were displayed on a semi-silvered mirror mounted horizontally between the subject’s eyes and their hands (Fig. 1A). The digitizing tablet (GTCO CalComp Inc., Columbia, MD, USA; 0.915 m × 0.608 m; accuracy 0.127 mm) captured the movement of a stylus that the subjects held in their hand over the surface of the tablet. The apparatus and the subjects were shrouded by a black drape, which blocked all external sources of light during experiments and prevented vision of the arm at all times. No other visual landmarks were available to the subjects and the only visual input available was what we displayed on the monitor. The monitor displayed visual targets 7 mm in diameter, which reflected from the mirror and appeared to be on the surface of the tablet in the plane of the subject’s hand movements. Images on the monitor were produced by a Visual Stimulus Generator (VSG, Cambridge Research Systems, Rochester, UK) PC card, which was programmed using MATLAB 7.5 (The Mathworks Inc., Natick, MA, USA). Custom-written software controlled the display of the targets, recorded and stored stylus positions at 100 Hz, and presented a cursor, the location of which was based on the stylus position on the tablet. The cursor location was computed every 10 ms and updated on the screen with 5-17 ms delay. The lower value includes a 3 ms response time of the LCD monitor plus a 2 ms delay to digitize stylus position, convert to screen coordinates, and transmit the graphics instructions to the monitor. The upper value adds to the lower value the maximal 12 ms delay in showing the target due to the 85 Hz rate with which the monitor polls for the video input. None of the subjects reported perceiving the delay between the stylus and cursor locations during task execution.

Procedures

Thirty-two healthy right-handed human subjects (17 women, 15 men; mean age: 30) with normal or corrected to normal visual acuity participated in the study. They all gave informed consent prior to their
inclusion and were naïve to the objectives of the study. The present study was approved by the Human
Research Ethics Committee of the Faculté de Médecine, Université de Montréal and was carried out in
accordance with the ethical standards set by the Committee. Four out of 32 subjects were familiar with
the experimental apparatus from their participation in a previous study of reaching movements to visual
targets without any visuomotor transformations (Gritsenko et al. 2009).

Subjects were divided into four groups of 8 (M-VF, M-KR, C-KR, and N-KR), each of which per-
formed the experiment under different conditions outlined below. Subjects in group M-VF (Mirror
transformation with Visual Feedback group) were shown a cursor, which provided continuous visual
feedback of the reaching movement at all times throughout all trials. Subjects in groups M-KR (Mirror
transformation with Knowledge of Results group), C-KR (Control with Knowledge of Results group),
and N-KR (No mirror transformation with Knowledge of Results group) received no real-time cursor
feedback during the movement in all trials. Instead, the subjects received knowledge of results in the
form of a visual display of the final cursor position relative to the target at the end of each trial in which
there was no target jump. No knowledge of results was given to the group M-KR, C-KR, and N-KR
subjects in trials with the target jumps, to assess the degree to which responses to target jumps were
influenced by real-time visual feedback (c.f. M-VF group).

The experiment consisted of two data-collection sessions on separate days (Fig. 2A). During both ses-
sions all subjects made planar pointing movements to visual targets without direct vision of their arm.
During the first session, subjects were given time to familiarize themselves with the apparatus and task
requirements, and then performed a Baseline block of trials. Each trial began when a yellow start target
(T0) was displayed on the surface of the tablet centered on their body midline (T0, Fig. 1B). The sub-
jects positioned the tip of the stylus at the reflected visual image of T0 by moving the stylus along the
surface of the tablet. Because the subjects could not see their hand and only group M-VF subjects re-
ceived continuous real-time cursor feedback, palpable guides were attached to the surface of the tablet
to guide their hand to the starting position. These guides formed a broad “V” shape with the T0 location at the junction of the two guides. After the subjects reached T0, its color changed from yellow to green to give visual confirmation that they had entered the starting position. After a 2 s delay, T0 disappeared and a new green target appeared 15 cm away from the starting position in one of three locations: at 90° (straight ahead, Y axis, T190), 60° (T160) or 120° (T1120) direction relative to mediolateral axis (X axis, Fig. 1B).

All subjects were instructed to look at the visual targets, although eye movements were not measured during this study, and to move the stylus in the plane of the tablet with a consistent speed to the T1 target as accurately as they could. Consistent speed was maintained across sessions and subjects by providing color-coded feedback at the end of each trial. The T1 target changed color to red or blue if the peak velocity of the movement surpassed or fell below respectively the value of 0.5 m·s⁻¹ by more than 5% (Fig. 1C). The color of T1 stayed green if the peak velocity was within the outlined range. These color cues were only used to guide the subjects and all trials with various movement speeds were included in the analysis. The angle between the two arms of the V-shaped guide was wide enough (115°) that the subjects could not and did not use them to guide their movements to the T160 or T1120 targets.

In half of the trials during the Baseline block of the first session, the target abruptly changed location at the onset of arm movement by 10° clockwise (CW) or counter-clockwise (CCW) along the 15-cm arc centered on T0 (T2⁻¹⁰ and T2⁺¹⁰ respectively, Fig. 1B and 2B). This created a perturbation in the required direction of movement without changing movement amplitude. The onset of arm movement was detected when the stylus moved > 2 mm from the starting position, which triggered a change in target position on the screen between 5 and 17 ms later. These target jumps were consciously perceived by the subjects (Gritsenko et al. 2009). The sequence of trials with and without jumps and the direction of target jumps were presented in a randomized-block design. Each subject performed 5 sets of 60 trials
separated by short rest breaks, for a total of 300 trials in the Baseline block on the first day (50 trials with and 50 trials without a target jump to each of the three targets).

During the second day’s session, group M-VF and M-KR subjects first performed an Adaptation block (Fig. 2A). During this block a mirror transformation was applied along the Y axis centered on the body midline, i.e. the direction of reach toward $T_{1}^{90}$. To implement the mirror transformation both the real-time cursor feedback provided to the group M-VF subjects and the end-of-trial cursor feedback provided to group M-KR subjects had its X-axis coordinate transposed to the opposite side of the midline Y axis during all trials, so that the appearance of the $T_{1}^{60}$ target required a reach to the $T_{1}^{120}$ target position to move the cursor to the $T_{1}^{60}$ target, and vice versa (Fig. 2C). This means that for the $T_{1}^{60}$ and $T_{1}^{120}$ targets, subjects had to move their hand away from the visual target to an estimated mirror-transposed location on the opposite side of the body midline in order to move the cursor toward the visual target (group M-VF) or appear near the target at the end of the trial (group M-KR). This produced a mirror dissociation between the subjects’ hand movements and cursor movements toward the target (Fig. 2C). In contrast, because the mirror transformation was applied about the body midline (Y axis), the subjects had to continue to aim their reaching movements toward the visual location of the $T_{1}^{90}$ target to move the cursor to that target, while the mirror transform only influenced the visual display of any deviations of the cursor position on either side of the straight-line path between $T_{0}$ and $T_{1}^{90}$. The Adaptation block lasted until the initial directional error and the final positional error (see Analysis section) of the mirror-transposed movements were within the range of the Baseline block values for the same subjects for at least two out of three $T_{1}$ locations. These criteria indicated that at the end of the Adaptation block, subjects became sufficiently skilled at estimating the mirror-transformed location of the $T_{1}^{60}$ and $T_{1}^{120}$ targets that they could make reaching movements towards those virtual target locations with similar distributions of initial directions and final positions as when they reached...
to the corresponding actual visual target locations in the Baseline block. Group M-VF and M-KR subjects performed between 180 and 240 trials with the mirror transformation during the Adaptation block.

Group C-KR subjects did not experience the mirror transformation during the first block of trials in the second daily session. Instead of the Adaptation block, they first performed a Practice block of non-transformed pointing movements like those in the Baseline block to the three targets, except that no target jumps were presented. During this Practice block, the C-KR subjects performed equal numbers of trials to that performed by the group M-VF and M-KR subjects during their Adaptation block. Finally, group N-KR subjects did not perform the initial Practice block at the start of the second day’s session.

To terminate the second day’s session all 4 groups of subjects performed a Test block, during which target jumps were introduced according to the procedure described for the Baseline block. Group M-VF, M-KR, and C-KR subjects performed both unperturbed and target-jump trials under the mirror-transformation condition (Fig. 2D). This means that if the target first appeared at the 60° angle from the horizontal (T160) and then jumped clockwise to the 50° angle, the subjects had to redirect their reach movement CCW from the 120° direction to the 130° direction to compensate for the target jump and make the cursor reach the target (Fig. 2D). Both M-VF and M-KR subjects performed the Test block after adapting to the mirror transform. These two groups were designed to assess whether (M-VF) or not (M-KR) exposure to continuous visual feedback of cursor motions during the Adaptation block would influence their degree of adaptation to the mirror transform or their response to target-jump trials in the Test block. Group C-KR subjects performed the same number of trials before doing the Test block as M-VF and M-KR subjects but encountered the mirror-transform for the first time during the Test block. The C-KR group was designed to assess to what degree any changes of responses of M-VF and M-KR subjects to target-jump trials from the Baseline block to the Test block were due to their
prior adaptation to the mirror transformation during the Adaptation block or to the presence of the mirror transformation itself, or due to other non-specific effects such as fatigue or diminished attention.

Finally, group N-KR subjects performed both unperturbed and target-jump trials in the Test block without the mirror-transform dissociation between cursor position and hand position. Instead, during trials with target jumps group N-KR subjects were simply instructed to “correct” their reach trajectory in the direction opposite to the direction of the target jump (Fig. 2D), to reproduce the task conditions used by the Day and Lyon (2000) in our study. Unlike the other 3 groups, N-KR subjects were asked to apply a voluntary mirror transform only to their response to the target jump while otherwise making arm movements in the condition of a normal visuomotor association.

During the trials with target jumps groups M-KR, C-KR, and N-KR received no visual knowledge-of-results feedback about the success of their corrections. However, during the trials without target jumps, visual knowledge-of-results feedback was presented to all 3 groups to help preserve their reaching accuracy and to prevent a decay of adaptation to the mirror transformation in group M-KR subjects.

Group M-VF received mirror-reversed cursor feedback at all times in all trials. Each subject performed sets of 60 trials separated by short rest breaks, for a total of 300 trials in the Test block. Thus, all subjects performed equal numbers of trials with target jumps.

Analysis

Data analysis was carried out off-line using MATLAB. The hand displacement traces were low-pass filtered at 20 Hz and each trial was aligned to the onset of hand movement, which was detected online for triggering of target jumps (see Procedures). Target jumps occurred on average $11 \pm 6$ ms after the detected onset of movement.

During all blocks, final positional error and initial directional error were measured for each trial (Fig. 2E). The final positional error ($\epsilon_p$) was the absolute distance between the cursor location at the end of
movement, i.e. when velocity fell below 2% of maximum for each trial, and the visual target location. The initial directional error was calculated based on the tangential angle of the trajectory. The tangential angle is the direction of the instantaneous tangential velocity vector measured every 10 ms according to the following formula: \( \arctan \left( \frac{V_y}{V_x} \right) \), where \( V_x \) and \( V_y \) are respectively horizontal and vertical trajectory speeds estimated by differentiating cartesian coordinates of the trajectory. For example, the tangential angle of the trajectory illustrated in Fig. 2F is initially about 95° relative to horizontal, and as the trajectory curves to the right the tangential angle decreases to about 45° toward the end of movement. Compared to the conventional calculation of movement direction, i.e. the direction of the current hand location relative to the starting T0 location (Fig. 2F, “polar angle”), the tangential angle provides a more sensitive measure of the time course of the instantaneous directionality of hand displacement.

The initial directional error (\( \varepsilon_\alpha \)) was calculated using the formula \( \varepsilon_\alpha = \alpha_{50} - \alpha^{T1} \), where \( \alpha_{50} \) is tangential angle 50 ms after the start of movement and \( \alpha^{T1} \) is the angle of the desired movement direction toward the corresponding T1 target.

These measures were made in the coordinate framework of the visual feedback provided to the subjects that they used to guide their movements in all trial blocks. In trial blocks in the normal visuomotor association, these measures were also collinear with the spatial location of the hand. In blocks of mirror-transformed trials, visual cursor position was mirror-transposed to the other side of the body midline from the current hand position.

For statistical analysis of adaptation to the mirror transformation by group M-VF and M-KR subjects, initial directional error, final positional error, and reaction times measured during the Adaptation block were averaged over each successive 10 trials per subject per T1 location. Only the first 180 trials performed by all subjects during the Adaptation block were included in this analysis. Statistical analysis of these measures was performed using three repeated-measures (RM) ANOVA tests with 3 factors: Group (2 levels: groups M-VF and M-KR), Bin (6 levels: six bins of 10-trial averages during the Adaptation block).
tation block), and T1 (3 levels: T1<sup>60</sup>, T1<sup>90</sup>, and T1<sup>120</sup>) using SYSTAT 11 (SYSTAT Software Inc, San Jose, CA, USA). These ANOVAs examined the differences between adaptation to the mirror transformation by the group M-VF and M-KR subjects. When the sphericity assumption of ANOVA was violated, the Greenhouse-Geisser correction for sphericity violation was used. Significant effects/interactions were explored using RM t-tests (α = 0.05) with Sidak-Bonferroni correction (Abdi 2007).

Analysis of responses to target jumps was done using both tangential and polar angles, both of which were calculated every 10 ms from the mean trajectory for each subject for each condition (Fig. 2F). The onsets of trajectory deviations in the same spatial (i.e. CW or CCW) direction as the jumped target (non-mirror corrections) were determined using the following method. First, the tangential or polar angles of mean trajectories in trials with CCW target jumps were subtracted from those in trials with CW target jumps for each T1 location per subject per condition (Fig. 3A-C). This increased the likelihood that even small opposite deviations of the CW and CCW trajectories are detected. A positive difference between trajectories represents a correction in the same direction as the target jump, while a negative difference represents a mirror-transformed correction in the opposite direction from the target jump (Fig. 3D). Second, the 95% confidence interval was calculated based on the initial 100 ms portion of the difference trace after movement onset (Fig. 3D, shaded rectangles). Third, the onset of non-mirror correction (trajectory deviations toward the target) was defined as the time at which the first positive value of a minimum 50-ms segment of positive deviations of the angular difference trace lay outside the confidence interval of the baseline trace. In some cases the onset of non-mirror correction was absent, i.e. the criteria mentioned above were not fulfilled. These cases were treated as missing values during statistical analysis of non-mirror correction onset times.

The onset of mirror correction, i.e. correction in the opposite direction from the target jump, was defined as the time of the peak amplitude of the non-mirror correction, that is, the start of the first 50-ms
segment of progressively smaller positive deviations of the difference trace after the onset of non-mirror correction (Fig. 3B & C, dashed lines). This corresponds to the time at which the difference in the reach trajectories during target jump trials in the CW and CCW directions shows the largest separation in the non-mirror direction and begins to reverse in the mirror direction. When this method was applied to tangential angles, it found earlier onsets of mirror corrections than when it was applied to the polar angles. This is because the tangential angle is based on a derivative of position, i.e. the direction of a velocity vector. This method, when applied to tangential angles, is equivalent to the algorithm described by Day and Lyon (2000), which relied on the peak lateral velocity (e.g. the rate of change of movement deviation from the straight-line path to the target) for determination of the onset of mirror corrections. Both of these methods represent a conservative estimate of the onset of mirror correction, because they include the time needed to decelerate the initial non-mirror correction before beginning to deviate the hand in the mirror direction. When the onset of non-mirror correction was absent, the onset of mirror correction was calculated as the time of the first negative value of a 50-ms segment of negative deviations that lay outside of the baseline confidence interval, beginning after the initial 100-ms baseline time interval. The onset of mirror correction was found in all cases, i.e. no missing values.

The amplitude of the non-mirror corrections in the Test block was calculated using two methods. The first method measured the difference in slopes of regression lines fitted to the first 100 ms of the polar angle traces following the onset of the non-mirror correction (Fig. 3B). The second method measured the peak difference between the tangential angles for CW and CCW target jumps at the end of the non-mirror correction (Fig. 3C & D). For those trials in which no significant non-mirror deviation was detected, the amplitude of the “non-mirror” response was measured as the largest positive deflection of the difference in tangential angles before the onset of the mirror correction, whether or not that value was within the baseline confidence interval. This amplitude was compared to the difference between the trajectory angles for CW and CCW target jumps at the corresponding time in the Baseline block.
Statistical analysis of the correction onsets was performed using repeated-measure ANOVA tests with 3 factors: Group (4 levels: groups C-KR, M-VF, M-KR, and N-KR), Condition (3 levels for onsets of non-mirror correction in Baseline block, non-mirror correction in Test block, and mirror correction in Test block), and T1 (3 levels as described above) using SYSTAT 11. Statistical analysis of the angular amplitudes was performed using repeated-measure ANOVA tests with 2 factors: Group (4 levels: groups C-KR, M-VF, M-KR, and N-KR) and T1 (3 levels as described above). The levels of the ANOVA on onsets tested for differences between the non-mirror onsets in baseline trials, non-mirror onsets in test trials, and mirror onsets in test trials. ANOVA on angular amplitudes tested for differences between the non-mirror angular amplitudes in test trials expressed as percentage of baseline trials across groups and T1 directions. Furthermore, statistical analysis of reaction times and peak velocities was performed using two more repeated-measures ANOVA tests with 2 factors: Group (4 levels) and Block (2 levels for Baseline and Test blocks). Correction for sphericity violation was done as described above. Significant effects/interactions were explored using RM t-tests with Sidak-Bonferroni correction.

Results

Baseline performance

All subjects were able to learn the task and to correct their trajectories for target displacements during the Baseline block of trials (Fig. 4). Summary descriptions of group conditions and subject reaction times and peak velocities of movement during the target-pointing task are found in Figure 2A and Table 1A, and statistical analysis of these variables is summarized in Table 1B. During the Baseline block of trials, the reaction times of group M-KR, C-KR, and N-KR subjects to the appearance of T1 were not significantly different. However, the reaction times of group M-VF subjects, who always received continuous real-time visual feedback of cursor position, were systematically shorter than those of group M-KR, C-KR, and N-KR subjects, who only received visual knowledge-of-results feedback of cursor
position at the end of each trial, by 52 ± 74, 49 ± 74, and 53 ± 39 ms mean ± SD values respectively, although this difference was significant only between group M-VF and N-KR subjects (Table 1B). No significant differences between peak velocities of subjects in different groups were found during the Baseline block (Table 1B, effect of Group within each Block).

In half of the trials during the Baseline block the target abruptly changed location at the onset of arm movement by 10° clockwise (CW, T2^−10) or counter-clockwise (CCW, T2^+10). As has been reported in many previous studies, all subjects responded to the target jump with a short-latency deviation of the original reach trajectory in the direction of the target displacement. These corrections were nearly equal in amplitude and opposite in direction in response to CW and CCW target jumps (Table 1A). These differences were not statistically significant (repeated-measures (RM) t-test between corrections for T2^+10 and T2^−10 target jumps during the Baseline block, across all movement directions: t = 0.83, 0.98, 0.12, and 0.85, p = 0.28, 0.24, 0.39, and 0.28 for groups M-VF, M-KR, C-KR, and N-KR respectively). This shows that trajectory corrections were symmetrical around the mean control trajectory.

The amplitude of trajectory corrections for the target jumps in the Baseline block was the largest in the M-VF group, followed by that of the N-KR, C-KR, and M-KR in descending order (Table 1A). Post-hoc analysis showed that there were no significant differences between the corrections of M-VF subjects and those of C-KR and N-KR subjects, but the differences between corrections of M-VF and M-KR subjects were significant (Table 4B, Baseline factor). Overall, this suggests that the presence of real-time visual feedback of cursor position is not necessary for the engagement of rapid online correction, although such feedback may increase the amplitude of the corrective response.

The onset latencies of trajectory corrections in the direction of target displacement (means ± s.d. across T1 locations: 201 ± 54, 243 ± 56, 271 ± 48, and 219 ± 22 for groups M-VF, M-KR, C-KR, and N-KR respectively) were not significantly different between all 4 subject groups, independent of whether or not they received real-time visual feedback of cursor position (Table 3A). The onset times were also
significantly shorter than the reaction times of the subjects to initial reaching movements toward T1 after its appearance (Table 1A; RM t-test: \( t = 5.42, 5.39, 3.96, \) and \( 7.38; p = 0.0001, 0.0001, 0.0014, \) and \( 0.0000 \) for groups M-VF, M-KR, C-KR, and N-KR respectively). Furthermore, the onset latency and the amplitude of the correction 100 ms after its onset were not significantly different in the first 12 target-jump trials (two replications of the two directions of target jump for all 3 targets) in the Baseline block compared to the last 12 target-jump trials for all 4 subject groups. This indicated that all subjects remained vigilant and showed no evidence of fatigue, habituation or any other change in their response to the target jumps during the course of the 300 trials of the Baseline block, including 150 target-jump trials.

The reach trajectories of the M-VF subject in Fig. 4A showed a clear tendency to converge at the target location at the end of the trial, including trials with target jumps. In contrast, the M-KR, C-KR, and N-KR subjects (Fig. 4B - D) showed more dispersion of their trajectories around the targets at the end of the trial. These subjective differences were supported by quantitative analyses. During the Baseline block the final position errors between the location of the cursor at the end of movement and the target location pooled across T1 locations were significantly smaller for the group M-VF subjects (0.6 ± 0.1 cm) than for groups M-KR (1.7 ± 0.7 cm), C-KR (1.5 ± 0.6 cm), and N-KR (1.8 ± 0.8 cm) in trials without target jumps. A post-hoc t-test showed that the differences between means were significant between the M-VF group and all other groups (\( t = 7.4, 7.5, \) and \( 7.0; p < 0.001 \) for M-KR, C-KR, and N-KR respectively), but not between the groups without real-time visual feedback (\( t = 0.3, p = 0.33 \) for M-KR vs. N-KR; \( t = 1.6, p = 0.11 \) for C-KR vs. N-KR; \( t = 1.4, p = 0.15 \) for M-KR vs. C-KR). This suggests that during the Baseline block M-VF subjects used the real-time visual feedback of hand position to improve their accuracy of pointing to the target compared to the groups without real-time visual feedback.

*Performance under the mirror transformation without target jumps*
The mirror transformation was applied for the duration of the Adaptation block for group M-VF and M-KR subjects, and only trials without target jumps were performed. The mirror transformation caused large initial movement direction errors (Fig. 5A) and final position errors (Fig. 5B) in the first few trials toward T1\(^{60}\) or T1\(^{120}\) targets in group M-VF and M-KR subjects. These errors were much smaller for movements toward the T1\(^{90}\) target, because the straight-ahead movements coincided with the axis of the mirror transformation. After only a few trials, all subjects quickly improved by decreasing both initial direction and final position errors. Group M-VF subjects showed somewhat smaller errors of both types in the first 10 trials after exposure to the mirror transformation than group M-KR subjects, although this difference was not significant (Table 2). Both the initial directional and final positional errors of both groups decreased at the end of the Adaptation block to within bounds of the 95% interval (2 SD) of Baseline values for two out of three target directions.

During the Test block, the initial directional and final positional errors in trials without target jumps were similar to those observed in the end of the Adaptation block (Fig. 5). This shows that group M-VF and M-KR subjects retained their adaptation to the mirror transformation during the Test block when target jumps were introduced together with the mirror transformation. However, the mean final positional errors in trials without target jumps during the Test block of group M-VF subjects were consistently larger than those recorded during their Baseline block (Fig. 5B). Instead, both position error amplitude, and position error variability of M-VF subjects with real-time cursor feedback during no-jump trials under the mirror transform of the Test block became similar to those of M-KR subjects without visual feedback. This suggested that the M-VF subjects were not able to use the continuous feedback about cursor position relative to the visual target as efficiently as during the Baseline trials to improve mirror-transformed reach accuracy.

The reaction time between the target appearance and the onset of hand movement increased abruptly during the Adaptation block compared to that during the Baseline block in both groups (Fig. 5C). The
reaction times of the group M-KR subjects did not change appreciably during the Adaptation block, while those of the group M-VF subjects decreased steadily for all target locations (Fig. 5C; Table 2). Similar results were obtained with 5-trial bins (data not shown). During the Test block, the reaction times of group M-VF and M-KR subjects remained higher than reaction times during the Baseline block.

During their Practice block, C-KR subjects pointed to visual targets for the same number of trials as the M-VF and M-KR subjects, but did not experience the mirror transformation. Their initial directional errors, final position errors and reaction times during the Practice block were not significantly different from their values in trials without target jumps in the Baseline block (RM t-test on final positional error: $t = 1.38, p = 0.18$; initial directional error: $t = 0.18, p = 0.86$; reaction times: $t = 1.13, p = 0.27$; data pooled across T1$^{60}$ and T1$^{120}$).

Group C-KR subjects encountered the mirror transformation for the first time during the Test block. Their movements in mirror-transformed trials without target jumps were similar to those of the M-VF and M-KR subjects when they first encountered the mirror transformation during their Adaptation block. Thus, the initial directional errors, final position errors and reaction times of C-KR subjects increased relative to their values in their Baseline and Practice blocks, and were not significantly different from those of M-VF subjects (RM t-test on final positional error: $t = 0.72, 1.20, 0.44, 1.60, 1.59; p = 0.48, 0.24, 0.66, 0.12, 0.12$; initial directional error: $t = 0.92, 1.05, 0.41, 0.94, 0.30; p = 0.37, 0.30, 0.68, 0.35, 0.76$; reaction times: $t = 0.44, 0.36, 0.08, 0.31, 0.08; p = 0.66, 0.72, 0.94, 0.76, 0.94$) and M-KR subjects (RM t-test on final positional error: $t = 1.42, 0.23, 1.58, 2.12, 1.07; p = 0.17, 0.82, 0.13, 0.04, 0.29$; initial directional error: $t = 0.42, 0.20, 0.93, 2.07, 2.21; p = 0.68, 0.84, 0.36, 0.05, 0.04$; reaction times: $t = 0.77, 1.51, 1.31, 1.53, 2.29; p = 0.45, 0.14, 0.20, 0.14, 0.03$) for bins 1 through 5 respectively during their Adaptation block. As a result, the C-KR subjects were well adapted to the mir-
ror transformation before the end of the Test block, similar to the M-VF and M-KR subjects at the end of their Adaptation block and during the Test block.

Unlike the other three groups, the N-KR subjects did not do an Adaptation or a Practice block prior to the Test block during the second daily session. However, the N-KR subjects did not show any disadvantage in task performance compared to the other groups because of less practice in the task before doing the Test block, nor any advantage because of fatigue, diminished attention or other factors experienced by the other groups because they did the Adaptation or Practice block before starting the Test block. For instance, no statistical differences between the Baseline and Test blocks of the N-KR subjects were found by RM t-tests on the initial directional errors (t = 0.18, p = 0.86), final position errors (t = 0.28, p = 0.78), and reaction times (t = 1.06, p = 0.30). Similarly, during the Test block, both initial directional and final positional errors were very similar between the group N-KR and M-KR subjects. The initial directional errors during the no-jump trials were 8.96 ± 3.2 and 9.04 ± 3.7° and the final endpoint errors during the same trials were 1.92 ± 1.1 and 1.96 ± 0.8 cm for the group N-KR and M-KR subjects respectively. Post-hoc t-tests showed that these differences were not significant (t = 0.09, p = 0.40 for the directional errors; t = 0.18, p = 0.39 for the positional errors). This shows that both N-KR and M-KR groups achieved similar performance levels in the no-jump trials of the Test block.

**Performance under the mirror transformation with target jumps**

To study the effect of the mirror transformation on the online correction mechanism, we compared trajectories during trials with target jumps in the Baseline and Test blocks (Fig. 6, 7). The amplitudes of the non-mirror corrections during the Test block were similar in amplitude and opposite in direction for CW and CCW target jumps (Table 1A).

Group N-KR subjects did not experience the mirror-transformed environment. Instead, during the Test block they reached toward the visual location of T1, but were instructed to respond to target jumps by deviating the reach trajectory in the direction opposite to the target jump, similar to the paradigm of
Day and Lyon (2000). Despite that verbal instruction, group N-KR subjects consistently showed an initial correction in the direction of the target jump (non-mirror correction) followed by a reversal of movement direction in the opposite direction (mirror correction) as illustrated by a representative subject’s trajectories in Fig. 6D and Fig. 7D. The amplitude of the initial non-mirror correction was similar for all three T1 targets.

Group M-VF, M-KR, and C-KR subjects, who performed the Test block with the mirror transformation, showed no evidence of a systematic mirror reversal of their initial rapid response to target displacements. Instead, they still often made initial non-mirror trajectory corrections followed by mirror corrections. However, the amplitude of the non-mirror corrections in group M-VF and M-KR subjects was reduced, to zero in some subjects, for movements toward the oblique T1$^{60}$ and T1$^{120}$ targets (Fig. 6A & B and Fig. 7A & B). Moreover, even in group C-KR subjects who did not receive prior exposure to the mirror transformation during their Practice block, the amplitude of the non-mirror corrections was substantially reduced for movements toward the oblique targets (Fig. 6C and Fig. 7C). During movements toward the oblique targets, 4 out of 8 group M-KR subjects, 2 out of 8 group M-VF subjects, and 2 out of 8 group C-KR subjects showed no detectable non-mirror corrections for at least one of the two oblique movement directions, while all group N-KR subjects showed detectable non-mirror corrections for both oblique movement directions. Furthermore, all group M-VF, M-KR, and C-KR subjects continued to show an initial non-mirror correction in response to T1$^{90}$ target jumps, but the amplitude of the response appeared to be smaller than that seen during the Baseline block before application of the mirror transform. These subjective observations were supported by quantitative analysis.

**Group analysis**

Group analysis of the timing of online corrections was based on individual onset times of mean trajectory deviations both toward and away from the new target location, i.e. onsets of non-mirror corrections in the Baseline and Test blocks (vertical black and grey lines in Fig. 7 respectively) and onsets of mir-
ror corrections in the Test block (vertical green lines in Fig. 7) (Fig. 8A). The onset times of measurable non-mirror corrections during the Test block were not significantly different from those of the Baseline block across the three target locations and groups of subjects (Table 3A). The onset time of mirror corrections was later than that of non-mirror corrections by $113 \pm 51$ ms on average across target directions and all four subject groups (Fig. 8A), a statistically significant difference (Table 3B, Levels 1/2 and 2/3). Furthermore, the onset times of mirror corrections were also not significantly different between the three target locations and subject groups (Table 3A). This shows that the timing of subjects’ behavior was not affected by the exposure to the mirror transformation (group N-KR versus groups M-VF, M-KR, and C-KR), nor by the availability of real-time visual feedback of cursor position (group M-VF versus M-KR and C-KR).

To quantify the amplitude of non-mirror trajectory deviations in the direction of the target displacements, the maximal difference between trajectory angles in trials with CW and CCW target jumps during the Test block was compared to that during the Baseline block at the corresponding time after the onset of movement (see Methods). Group N-KR subjects showed non-significantly smaller amplitudes of non-mirror corrections during the Test block compared to those measured at the same time post movement onset during the Baseline block (Table 4) and those amplitudes were equal across the three movement directions (Fig. 7A and 8B, black symbols). Note, that the post-hoc test used to evaluate significance of these changes takes into account the correlation between the repeated measurements and diminishes the statistical effect of between-subject variability. Thus, statistically insignificant change in the amplitude of non-mirror corrections in the Test block cannot be explained by the large between-subject variability of the N-KR group (Fig. 8B, D). Furthermore, the amplitude of the non-mirror corrections in the beginning of the Baseline block were not significantly different from those in the beginning of the Test block (RM t-test between Baseline block and first 2-trial means of the Test block, across all target locations: $t = 0.52, p = 0.35$). Also, the amplitude of the non-mirror corrections
of N-KR subjects became significantly smaller over the course of the Test block (RM t-test between first and last 2-trial means in the Test block, across all target locations: t = 2.47, p = 0.02; Fig. 8E), but not in the course of the Baseline block (c.f. Baseline Performance section). This indicates that a partial reduction of the amplitude of the rapid non-mirror online correction in the N-KR group that was equal across all target directions began to emerge in the course of practicing voluntary mirror responses to the target jumps during the course of the 300-trial Test block without an overall mirror transformation.

Following 180-240 trials of practice with the mirror transformation, groups M-KR and M-VF subjects showed no evidence for a reversal of sign of the early response to the target jump during the Test block (Fig. 7A,B). Instead, drastically reduced non-mirror corrections were observed compared to their responses to target jumps in their Baseline block, and compared to those of the N-KR group during their Test block (Table 4A). Post-hoc analysis showed that during the Test block only the N-KR group was significantly different from the other groups (Table 4B). This shows that the non-mirror trajectory corrections decreased similarly in all groups that experienced the mirror transformation in the Test block. This decrease in non-mirror response to the target jumps was larger for oblique movements (toward T1\(^{60}\) and T1\(^{120}\) targets). Post-hoc analysis showed that for oblique movements the post-adaptation decrease of the amplitude of non-mirror corrections relative to Baseline was significant for M-KR, M-VF, and C-KR groups, while for the straight ahead movements this decrease was non-significant for only the M-VF and C-KR groups (Table 4C). Also, post-hoc tests across target directions showed that the non-mirror corrections during the Test block were significantly different between oblique and straight-ahead movement directions, but only for the group M-VF subjects (Table 4D). These findings show that following exposure to the mirror transformation there was a selective suppression of the rapid online non-mirror correction response in a task-specific manner. Furthermore, this suppression was not dependent on the presence of real-time cursor feedback. Lastly, even in the first two target-jump trials for each of the three T1 targets of the Test block group M-KR and M-VF subjects showed significantly
reduced non-mirror corrections (RM t-test between Baseline block and first 2-trial means of the Test block, across all target locations: \( t = 2.37, p = 0.03 \) for group M-KR; \( t = 6.94, p < 0.001 \) for group M-VF). During the Test block the amplitudes of non-mirror corrections did not change significantly in group M-KR and M-VF subjects (RM t-test between first and last 2-trial means in the Test block, across all target locations: \( t = 2.02 \) and 1.76, \( p = 0.05 \) and 0.09 respectively). This shows that the task-specific suppression of the rapid non-mirror online correction appears immediately after the Practice block at the start of the Test block with the mirror transformation. In contrast, N-KR subjects made larger non-mirror corrections than the other subjects at the start of their Test block and showed evidence of a smaller reduction in the non-mirror response that emerged slowly during practice of making voluntary mirror responses to the target jumps.

The immediate appearance of the task-specific suppression of the non-mirror correction in group M-KR and M-VF subjects suggests that this suppression is dependent on the prior adaptation to the mirror transformation. However, the amplitudes of the non-mirror corrections of the C-KR subjects, who were not exposed to the mirror transformation during their Practice block, were very similar to those of the M-KR subjects from the outset of their Test block (Fig. 8, Table 4). Group C-KR subjects showed significantly reduced non-mirror corrections in the first two trials of the Test block (RM t-test between Baseline block and first 2-trial means of the Test block, across all target locations: \( t = 2.48, p = 0.02 \)) as did group M-KR subjects (see above). This suggests that the task-specific suppression of the rapid non-mirror corrections does not depend on the prior adaptation to the mirror transformation during the Adaptation block. Instead, it appeared in C-KR subjects as soon as they began to perform the reaching movements under the mirror transformation.

The same pattern of similar onset times but reduced amplitude of initial non-mirror corrections followed by a delayed mirror correction in the Test block compared to the Baseline block was observed when the slope of initial trajectory deviations were used for the analysis (Fig. 8C, D).
Discussion

The neural mechanisms controlling reaching movements include a rapid online correction mechanism that compensates for unexpected target displacements by causing a rapid deviation of the ongoing reach trajectory in the spatial direction of the target displacement (i.e., a non-mirror correction) (Elliott and Allard 1985; Pelisson et al. 1986; Prablanç and Martin 1992). One of the two principal findings of this study was that, after a short period of motor adaptation to a mirror-image transformation of visual feedback of the real-time trajectories or final endpoints of reaching movements to stationary targets, there was no evidence of a corresponding mirror transformation of the directionality of the rapid online correction mechanism. Instead, there was a selective decrease in the amplitude of the initial rapid online correction response. The suppression of the early online correction was the strongest, and in some subjects nearly complete, for the oblique movement directions in which the transformation caused the largest spatial dissociation between the visual input guiding behavior (target location and cursor movement/final position) and the physical response (direction of reaching movement and its associated proprioceptive afferent feedback). The suppression was not as strong for movements to the T1⁹₀ target, which corresponded to the axis across which the mirror transformation was applied, and which required reaching movements aimed at the visual image of the target. In this case, unlike for the oblique targets, the final physical hand position corresponded to the visual spatial location of the target, and the mirror transformation was only evident for the lateral deviations of the reach trajectory on either side of the straight-line path between the T₀ and T₁⁹₀ positions.

The second principal finding was that a similar substantial reduction in the amplitude of the initial rapid non-mirror online correction response to target jumps was seen in C-KR subjects as soon as they began to make reaching movements in the mirror-transformed condition and before they were fully adapted to the transformation itself. As for M-VF and M-KR subjects, the degree of reduction was greater for the oblique T₁⁶₀ and T₁¹²₀ targets than for the straight-ahead T₁⁹₀ target.
Furthermore, the latency of the non-mirror responses shown by all subjects during the Test block was the same as the latency of their responses to target displacements in the Baseline block. In addition, during movement with the mirror transformation the non-mirror correction of the reach trajectories by group M-VF, M-KR, and C-KR subjects was followed by the mirror correction at a latency that coincided with the onset time of voluntary mirror-image modifications of arm trajectories in response to explicit instructions (group N-KR; c.f. Day and Lyon 2000). Each of these results and their implications are discussed below in more detail.

Plasticity of online correction

The current study focused on a specific aspect of motor learning, namely whether or not the rapid online correction mechanism would show adaptive changes that would parallel the subjects’ acquisition of the ability to perform voluntary reaching movements while exposed to a visuomotor perturbation that mirror-reflected visual feedback of hand movement in the mediolateral direction across the body midline. We found that the subjects in groups M-VF and M-KR became quite adept at aiming their reaching movements to a mirror transposed location relative to a visual target after a short period of practice. However, the early online correction evoked by a target jump after reaching onset did not reverse together with the reversal of visual feedback, as would be expected from a complete adaptation to the transformation. This supports the findings of other studies that the early online correction mechanism responsible for driving the hand toward the visual target is a highly automated process that is relatively insensitive to voluntary control during short periods of practice (Castiello et al. 1991; Cressman et al. 2006; Day and Lyon 2000; Gomi 2008; Johnson and Haggard 2005; Johnson et al. 2002; Pelisson et al. 1986; Prablanc and Martin 1992). While reversal of the fast online correction process may be unachievable during a short period of practice, as found in this study, the contribution of this process to the online control of movement can be modified, e.g. scaled down, as shown by our results.
These findings reveal a clear functional dissociation between the planning of voluntary arm movements and rapid online correction mechanisms following a short period of adaptation to a mirror transformation in M-VF and M-KR subjects. After 180-240 trials of practice, the subjects could successfully make voluntary reaching movements to a spatial location that was mirror-transposed from the spatial location of the visual target and visual feedback of arm movements. However, there was no corresponding reversal of the mapping between sensory input and motor output in the rapid online correction mechanism, only a partial or nearly complete suppression. It is possible that more extensive practice with the mirror transform might result in the complete adaptation of the rapid online correction mechanism for reaching movements, so that mirror responses begin at the usual short latency rather than after a further delay.

Furthermore, we found that even without prior exposure to the mirror transformation (group C-KR) there was a substantial suppression of the early non-mirror online correction response to target jumps during movements toward the oblique targets, in which the experienced visuomotor dissociations were the largest, in the first two target-jump trials to each target after the application of the transformation. This suggests that the amplitude of the non-mirror online correction response may be rapidly suppressed while making reaching movements to visual targets in a mirror-transformation condition, even before the subjects have fully adapted to the transformation itself. This suppression may be a general effect of subjects’ explicit and implicit learning strategies used to adapt to the mirror-transformed condition (Mazzoni and Krakauer, 2006). The subjects may have initially relied on an explicit strategy to compensate for the mirror transformation in the beginning of the Adaptation or Test block, which caused a rapid suppression of the rapid non-mirror corrections. Then, with repetition they may have gradually developed an implicit strategy, characterized by a gradual decrease in the movement reaction times (Fig. 5C).
Alternatively, the suppression might have resulted more specifically from the dissociation between the visual and proprioceptive feedback caused by the mirror transformation, which could disrupt the estimate of current limb state that is believed to be required by the rapid online correction mechanism to generate corrective responses (Saunders and Knill 2003; van Beers et al. 1996; Wolpert and Kawato 1998; Wei and Kording 2009; for reviews see Paillard 1996 and Shadmehr and Krakauer 2008). In contrast to the fast online correction mechanism, the delayed mechanism responsible for mirror corrections may involve a more complex comparison between the afferent and efferent signals for the calculation of a task-specific error, which would drive adaptation to the mirror transformation (Heath et al. 2009; Magescas et al. 2009). In our study, subjects were required to move to an estimate of the mirror target location either under combined, but dissociated, online visual and proprioceptive guidance (group M-VF) or only under online proprioceptive guidance with visual knowledge of results at the end of the movement (groups M-KR and C-KR). The task-specific error that would help subjects reach with the mirror transformation would require a recalculation of either the visual target position into the corresponding mirror target position, or the current hand position into the corresponding mirror hand position, so that the hand and target state signals are in a common reference frame and could be directly compared. Additional computations required for the task-specific error correction may explain the 110 ms delay between the onset of non-mirror and mirror corrections observed in our study (Fig. 8A). To summarize, our results are consistent with the idea that the early and late online correction are governed by two pathways that include direct and task-specific errors respectively. The parietal cortex may be involved in calculating the two proposed types of errors during adaptation to the visuomotor transformation, as suggested by studies of motor deficits in people with parietal damage and by imaging studies of cortical activity during execution of visuomotor remapping tasks (Clower et al. 1996; Ghilardi et al. 2000; Inoue et al. 1997; Newport et al. 2006; Rossetti et al. 1998).
In contrast, the initial non-mirror responses of the N-KR subjects were significantly larger than those of the other 3 groups at the start of the Test block and remained larger for the duration of the Test block. This finding is consistent with the results of Day and Lyon (2000). It confirms that the rapid online correction mechanism is relatively insensitive to modification by the application of an arbitrary voluntary visuomotor dissociation to attempt to move the hand in the direction opposite to the direction of a target jump while performing reaching movements in the usual veridical visuomotor association. The N-KR subjects show that the non-mirror responses persist for at least 150 trials with target jumps. This stands in striking contrast to the behavior of the other 3 groups of subjects, who showed a substantial reduction in the amplitude of the initial non-mirror responses while making reaching movements in the context of a mirror transformation. The larger initial non-mirror responses of N-KR subjects also indicate that the reduced slope and peak amplitude of the non-mirror responses of M-VF, M-KR, and C-KR subjects at the time of the onset of the delayed mirror correction is not simply due to the mechanical effect of decelerating the limb before beginning to move in the mirror transformed direction. Despite having to reverse their initial non-mirror response, the N-KR subjects still showed larger initial non-mirror response to target jumps than that of the other subject groups, including the C-KR subjects, who like the N-KR subjects encountered the transformation for the first time in the Test block. This further supports the conclusion that the reduced size of the early non-mirror responses of the M-VF, M-KR, and C-KR subjects were due to the global application of the mirror transformation to their visuomotor behavior and not just to their responses to the target jumps.

Nevertheless, repeated exposure of N-KR subjects to the target jumps without the mirror transformation in the course of their Test block caused a small but significant decrease of the amplitude of the initial non-mirror corrections (Fig. 8E). This shows that repeated practice of the “voluntary” mirror correction may result in a gradual reduction of the initial rapid non-mirror response to the target jumps. This plasticity may be mediated by either a gradual decrease in the gain of the rapid online correction
process, or a gradual substitution of an explicit “voluntary” strategy by an implicit adaptation (Mazzoni and Krakauer, 2006), or both.

A potential confound of the comparison of results across groups is that group N-KR did not do an Adaptation or Practice block and thus performed fewer trials overall on the second day than the number of trials performed by the M-VF, M-KR, and C-KR groups. The additional Adaptation or Practice block may have led to fatigue of subjects in the latter groups, which could have contributed to the observed between-group differences in the amplitudes of early online correction. Although we cannot completely rule out fatigue or inattention as a factor in the reduced non-mirror responses of M-VF, M-KR, and C-KR subjects, other lines of evidence suggest that subjects did not find these tasks particularly fatiguing. First, all blocks were done in sub-blocks of 60 trials with brief rest periods in between. We found no changes in the kinematics of reach trajectories during trials without target jumps, and no changes in the amplitude and timing of the rapid online correction to target jumps from the beginning to the end of the Baseline blocks in all 4 subject groups. The initial non-mirror responses of N-KR subjects persisted, albeit with a somewhat reduced amplitude, for the duration of the 300-trial Test block, but the much larger reduction of the non-mirror response in the M-VF, M-KR, and C-KR subjects was evident in the first trials of the Test block following the shorter 180-240 trial Adaptation or Practice blocks. Finally, there were no differences in the initial movement direction, final endpoint position, or reaction times during Test-block trials without target jumps, between the N-KR group and the other 3 groups who performed the extra trials of the Adaptation or Practice block. These various lines of evidence suggest that fatigue or inattention were not the major confounding factors in the performance of the subjects, who appeared to remain consistently vigilant throughout the duration of both experimental sessions.

Note, that there are two ways to view the nature of the mirror transformation. One is that the task is constant in the extrinsic spatial coordinates of the visual targets and cursor feedback, and the subjects
learn to produce mirror-transformed arm movements in response to the oblique targets T1^60 and T1^120. Alternatively, the task is constant in the intrinsic motor space of the arm movements, and the subjects learn to generate a given oblique movement in response to a mirror-transposed visual target. Our data does not allow us to distinguish between these two possibilities, or whether different subjects applied one or the other of these two scenarios and whether this had any impact on their performance of the task.

**The mechanism of rapid online correction**

Our results suggest that the mechanism of trajectory correction during movement with the mirror transformation consists of at least two error-correction pathways with different delays (Alstermark et al. 1990; Alstermark et al. 1987; Day and Lyon 2000). The first is a short-latency “automatic” online correction mechanism that was highly sensitive to the spatial direction of displacement of the target, and the second is a long-latency “voluntary” mechanism that applied the arbitrary sensorimotor mappings between sensory input and motor output. This latter process may also be responsible for planning the initial reach trajectories to T1 targets under the mirror transform. We found that the subjects showed a larger reduction in their early non-mirror online correction for oblique movement directions and a smaller reduction for the T1^90 movement direction. Furthermore, the onset times of both early and late corrections stayed constant across both pre- and post-Adaptation/Practice blocks, and in all subject groups. This suggests that the two correction pathways do not compete against each other, but instead are independent pathways, each with its own loop delay. Moreover, rapid online corrections occurred at the same time and were of the same magnitude in M-KR, C-KR and N-KR subjects as in M-VF subjects in the Baseline block. This showed that the rapid online correction mechanism can be engaged when subjects have only proprioceptive feedback and possible efference copies of outgoing motor commands but no visual feedback to estimate limb state during movement (Gritsenko et al. 2007, 2009; Gosselin-Kessiby et al. 2008, 2009).
The rapid online correction mechanism is often suggested to rely on the error calculated between the estimates of arm state and goal state (Bhushan and Shadmehr 1999; Mehta and Schaal 2002; Nijhof 2003; Sabes 2000; Sarlegna et al. 2003, 2004; Shadmehr and Krakauer 2008; Wolpert and Kawato 1998). According to this hypothesis, the fast online correction mechanism responsible for non-mirror corrections in our study calculates the error signal by directly comparing the earliest estimate of arm state, derived mainly from proprioception and an efference copy of the outgoing motor command in M-KR and C-KR subjects, but complemented by the visual cursor input in M-VF subjects (Bard et al. 1999; Davidson and Wolpert 2005; Desmurget and Grafton 2003; Gordon et al. 1995; Sabes 2000; Sarlegna et al. 2003, 2004, 2006; Wolpert and Flanagan 2001), and the earliest estimate of target state derived from visual or efferent eye-movement signals about the initial target location and any change in the target’s location (Elliott and Allard 1985; Lemay and Proteau 2001; Pelisson et al. 1986). Based on this error, a target jump would then elicit the appropriate rapid compensatory adjustment to the outgoing motor command in the Baseline block. Multiple studies suggest that the posterior parietal cortex might be involved in combining multisensory information to produce a current arm state estimate for the generation of the rapid online correction (Battaglia-Mayer et al., 2000; Della-Maggiore et al. 2004; Desmurget et al. 2001; Goodale and Milner, 1992; Kalaska et al., 1983; Mulliken et al. 2008; Pisella et al 2000).

This direct-error pathway worked efficiently when the sensory inputs and motor output commands had their usual veridical relationship in the Baseline block. During movements performed under the mirror transformation in our study, however, this mechanism would sense an increasing error between the physical hand position signaled by proprioceptors and the visual target position. However, this direct error cannot be used for online correction, because instead of approaching one of the oblique visual targets (T160 or T1120) the hand had to physically move away from it under the mirror transformation, i.e. subjects had to move toward an estimated target location on the opposite side of their midline in
order for the cursor to move toward the visual target location. In contrast, for the straight-ahead direc-
tion (T190 target) the hand always moved toward the visual target and the direct error between the pro-
rioceptively-signaled hand position and visual target location could still be used for correcting for the
component of the error between hand position and visual target location along the axis of the move-
ment direction, but not for the any errors perpendicular to the axis of movement direction. Therefore,
the unequal usefulness of the direct error for controlling movements toward straight-ahead and oblique
targets may drive unequal suppression of the early online correction mechanism that relies on this type
of error during reaching with the mirror transformation. The suppression of gain could result from a
disruption of the usual neural computations within the state estimation mechanism, because of the non-
veridical relationship between the proprioceptive and visual input and motor commands under the mir-
ror transformation. Alternatively, it could also result from an attempted explicit volitional suppression
of the online correction mechanism by the subjects because the non-mirror responses were inappro-
priate. Either mechanism would be less likely or less prominent in N-KR subjects for whom the usual
veridical relationship between proprioceptive and visual inputs and motor outputs applied during their
reaching movements to all targets, except in response to the target jumps. As a result, their initial non-
mirror responses to target jumps were much less reduced in size by their attempts to apply a voluntary
mirror transform to their target jump responses than was the case for the three other subject groups in
the Test block.

Role of vision in online correction and adaptation

The contribution of vision to online control can be subdivided based on its role in the estimation of tar-
get location or hand position. In the former role, vision of the target throughout the whole movement
has been shown to increase reaching accuracy by providing a continuous reliable signal of the move-
ment goal (Desmurget et al. 1997; Elliott and Allard 1985; Favilla et al. 1989; Lemay and Proteau
2001; Pelisson et al. 1986; Rossetti et al. 1994; Schweickert 1992; Wing 1992). Furthermore, in our
study, M-VF, M-KR, and C-KR subjects showed a prolongation of movement reaction times under the mirror transformation of the Adaptation and Test blocks compared to their reaction times during the Baseline block. In contrast, the reaction times of N-KR subjects did not change between Baseline and Test blocks. The added delay in movement onsets for M-VF, M-KR, and C-KR subjects presumably reflected the extra time required to plan and initiate the rotated reaching movements to a mirror-transposed reaching goal.

In the latter role, vision of the hand during movement increases reaching accuracy by contributing to the estimation of limb state during movement (Abahnnini and Proteau 1999; Blouin et al. 1993; Carlton 1981; Ghez et al. 1995; Paillard 1996; Saunders and Knill 2003; van Beers et al. 1996; Sarlegna et al. 2003, 2004). Consistent with that literature, results of our study show that during Baseline blocks group M-VF subjects, who received online visual feedback of their hand position, had shorter reaction times to the appearance of the visual targets (Table 1A, Fig. 5C) and yet still reached the targets with better accuracy than group M-KR (Fig. 5B) or group C-KR and N-KR subjects. This shows that M-VF subjects could benefit from the visual representation of hand position during movement to enhance their performance, both in terms of faster reach onsets and smaller final position errors.

Could online visual feedback also enhance adaptation to visuomotor transformations? We found that group M-VF subjects did show consistently smaller mean errors during the early exposure to the mirror field (Fig. 5A,B). This in part reflected the advantage of having real-time feedback of cursor position, which allowed M-VF subjects to see and respond to the mirror transformation even during the course of the first movements in the Adaptation block. In contrast, M-KR subjects only received visual input about the mirror transformation at the end of each trial. Moreover, the reaction times of M-VF subjects decreased significantly faster than those of M-KR subjects (Fig. 5C). The progressively decreasing reaction times shown by the M-VF subjects suggest that the availability of continuous visual feedback during movement may have allowed those subjects to rely increasingly on visual online correction to
ensure successful task performance during adaptation to the mirror transformation. Alternatively, the continuous visual feedback may have facilitated the adaptation of predictive feedforward planning processes before movement onset in M-VF subjects. However, both position error amplitude and variability of M-VF subjects did not return to baseline values after adaptation to the mirror transformation and, instead, became similar to those of the M-KR and C-KR groups. The reduced gain of the rapid online correction mechanism might have contributed to this increase in endpoint position errors of M-VF subjects during trials without target jumps in the Test block, compared to their performance in the Baseline block. This suggests that the continuous visual cursor feedback with the applied mirror transformation could not be used as efficiently to reduce the endpoint error compared to movement with veridical cursor feedback. Overall, this suggests that continuous visual feedback of the cursor during movements with the mirror transformation appeared to have relatively little effect on the responses of M-VF subjects to target jumps compared to M-KR subjects, at least over the time course of a few hundred trials of exposure to the transformation (Adaptation and Test blocks) during a single daily session.

Pointing movements with the mirror transformation have some parallels with the widely studied antisaccade task, in which subjects are required to look away from the visual target (for review see Munoz and Everling 2004). The key difference is that in a true anti-saccade task, the subjects must always move in the direction exactly opposite to the target location, that is, they must apply a mirror transform simultaneously about both the X and Y axes. In contrast, our mirror transform was implemented about the Y axis (the body midline) only. Nevertheless, it is likely that there are some similarities in the processes involved in anti-saccade generation as in the trajectory modifications in presence of the mirror transform. Consistent with this idea we found that the reaction times in trials with the mirror transform were longer than those in control trials (difference of 72 ms for group C-KR, 80 ms for group M-VF, and 119 ms for group M-KR, Table 1) by a similar amount as the difference between onset times
of the anti-saccades and those of the pro-saccades (difference of 60-90 ms; Fischer and Weber 1997; Guitton et al. 1985; Hallett and Adams 1980).

Conclusions

In conclusion, results of the study argue for two error-corrective pathways with different delays comprising online control of movement. Our results further suggest that the fast pathway relies on direct comparison between afferent and efferent signals of arm and target states for error correction, while the slow pathway includes a delayed “voluntary” task-specific error feedback. The study also found that visual representation of mirrored hand position is not necessary to elicit both early and late corrections. Finally, results of the study show that short-term practice of the mirror transformation that is sufficient to permit subjects to make voluntary reaching movements to spatial locations that are mirror transposed from the location of a visual target is not sufficient to completely reverse the fast online-correction pathway. Instead short periods of practice of reaching movements under mirror transformation can only rapidly reduce the contribution of the fast corrective pathway to the overall online control. These findings in turn suggest that adaptive processes for the planning and initiation of reaching movements under different visuomotor dissociations are at least partly independent of any mechanisms that might adapt the rapid online correction mechanism to those same visuomotor dissociations.
This research was supported by CIHR Postdoctoral Fellowship (V. Gritsenko) and CIHR Operating Grant MOP62983 (J. F. Kalaska).
References


Paillard J. Fast and slow feedback loops for the visual correction of spatial errors in a pointing task: a reappraisal. *Canadian journal of physiology and pharmacology* 74: 401-417, 1996.


**Figure legends**

Figure 1. Experimental paradigm. A. Schematic of the experimental setup. B. Coordinate system and target locations relative to the subject, T0 - starting location, T1\(^{60}\), T1\(^{90}\) and T1\(^{120}\) - initial target locations \(60^\circ, 90^\circ\) and \(120^\circ\) away from the X axis, T2\(^{10}\) and T2\(^{10}\) - examples of a jumped target location illustrating a \(10^\circ\) jump clockwise and counterclockwise respectively, relative to the T1 direction. C. Examples of tangential velocities of representative subjects in each group. Lines represent means; shaded areas outline s.d.; traces show mean velocities from trials in which the subject’s movements were indicated to be to fast (dashed line), to slow (dotted line), or with correct speed (solid line).

Figure 2. A. Block procedure table. Column labels indicate group acronyms. KR - knowledge of results; VF - visual feedback; M - mirror; C - control; N - no mirror; Pract. - Practice block, Adapt. - Adaptation block. B. Representative hand (thin solid line) and cursor (thick dashed line) trajectories with target jumps during Baseline block toward T1\(^{60}\) target; T0 - starting position; T1 and T2 - control and jumped target locations respectively. C. Hand and cursor trajectories toward the same T1 target as in B during the Adaptation block for M-VF and M-KR groups. Grey dashed circle indicates the location of the “virtual” target to which the subjects had to move. No target jumps were presented in this block. D. Hand and cursor trajectories toward the same targets as in B for a trial with a target jump during the Test block. Grey arrows show the direction of the “virtual” target jump, i.e. the desired direction of trajectory corrections. E. Control trajectory toward the T1\(^{90}\) target. Black arrows indicate how the directional and final positional errors were calculated. F. Illustration of the tangential and polar angle measurements for a sample point (white-filled dot) on the control trajectory.

Figure 3. Illustration of trajectory analysis. A. Examples of mean hand trajectories during Baseline (left column) and Test (right column) blocks. Dashed lines indicate trajectories with clockwise (CW) target jumps, solid lines indicate trajectories with counterclockwise (CCW) target jumps, grey dotted lines
show control trajectories without target jumps. Filled circles show initial target locations, open circles show jumped target locations. B. Polar angles of mean trajectories illustrated in A with the same line coding. Time zero is the onset of movement. Target jumped 5-17 ms after the onset of movement. Vertical black lines indicate onsets of non-mirror trajectory corrections, vertical grey lines delineate a 100 ms time interval after the onset. Angled grey lines show regressions fitted to the trajectories within the 100 ms time window. The difference in slope between the regressions for CW and CCW target-jump trajectories was used as one of the measures of the amplitude of trajectory correction. C. Tangential angles of mean trajectories illustrated in A with the same line coding. D. Angular difference trace calculated by subtracting tangential angles of trajectories with CW and CCW jumps. Grey shaded area indicates the duration of the difference trace used for baseline confidence interval calculation. Dotted vertical lines show the onset times of the mirror correction, estimated from the time of the peak positive (non-mirror) deviation of the angular difference curves in target displacement trials (D, right; see Methods).

Figure 4. Examples of hand trajectories in individual trials with target jumps in the Baseline block. Red lines indicate trajectories with CW (negative) target jumps, blue lines indicate trajectories with CCW (positive) target jumps, filled circles show initial target locations, open circles show jumped target locations. A, B, C, and D. Trajectories of group M-VF, M-KR, C-KR, and N-KR subjects respectively.

Figure 5. Adaptation to the mirror transformation by group M-KR and M-VF subjects. Data shown are only for trials without target displacements during the Baseline, Adaptation, and Test blocks. Lines show mean values from 10 consecutive trials without target jumps, shaded areas show s.e.m. across subjects. Grey box highlights values collected during the Adaptation block. A. Initial directional error per target position. B. Final positional errors per target position. C. Reaction times per target position. Plots show data for each movement direction with colors corresponding to data from M-KR (dashed line) and M-VF (solid line) groups.
Figure 6. Average hand trajectories from representative subjects in each group. A, B, C and D. Group M-VF, M-KR, C-KR, and N-KR subjects respectively. Filled circles indicate initial target positions, open circles indicate jumped target positions. Red and blue lines show mean trajectories from Baseline block, orange and cyan lines shows mean trajectories from the Test block; red and orange colors indicate CW (negative) target jump, blue and magenta colors indicate CCW (positive) target jumps.

Figure 7. Tangential angle of average hand trajectories shown in Fig. 6 for representative subjects from each group. The organization and color coding of trajectories is the same as in Fig. 6. Vertical lines indicate the onset times of non-mirror and mirror corrections during baseline (black line) and test (grey and green lines) blocks. Shaded areas indicate the difference between trajectories with the opposite target jump directions, which highlight corrections in the opposite direction from the intended trajectory corrections during the Test block.

Figure 8. Group analysis. A. Onset times (means across subjects ± SD) of mirror and non-mirror corrections during Baseline and Test blocks calculated based on the tangential angle, i.e. the instantaneous direction of movement (Fig. 3D). Symbols indicate target position: square - T1 60, circle - T1 90, triangle - T1 120. B. Amplitude (means across subjects ± SD) of non-mirror corrections during Test block expressed in percentage of the Baseline block, calculated based on the tangential angle. C. Onset times (means across subjects ± SD) of mirror and non-mirror corrections during baseline and Test blocks calculated from the polar angle (Fig. 3B). Symbols and colors are as in A. D. Amplitude (means across subjects ± SD) of non-mirror corrections during the test block, calculated from the slope differences fitted to the polar angle traces (Fig. 3B). Symbols and colors are as in B. E. Amplitude (means across subjects ± SD) of non-mirror corrections during early (filled symbols) and late (open symbols) parts of the Test block, calculated based on the tangential angle (left plot) and slope differences (right plot), expressed in percentage of the Baseline block. Blue symbols - group M-KR data, red symbols - group M-VF data, black symbols - group N-KR data.
Figure 1

A. Monitor and digitizing tablet setup.

B. Diagram showing angles and points T1, T120, T2, T2-10, T0, Y, X.

C. Graphs showing tangential velocity for different groups:
   - Group M-VF subject
   - Group M-KR subject
   - Group C-KR subject
   - Group N-KR subject

Graphs indicate velocity over time with three categories: Fast, Good, Slow.
Figure 2

<table>
<thead>
<tr>
<th></th>
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</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mirror</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Target jump</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cursor</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

| Pract/Adapt. |   |   |   | N/A |
| Mirror       | + | + | - | N/A |
| Target jump  | - | - | - | N/A |
| Cursor       | + | - | - | N/A |

| Test |   |   |   |   |
| Mirror | + | + | - | - |
| Target jump | + | + | + | - |
| Cursor  | + | - | - | - |

(A) Table showing groups and blocks

(B) Baseline block

(C) Adaptation block

(D) Test block

(E) Tangential angle

(F) Polar angle
Figure 3

A. Baseline block and Test block diagrams showing the tangential angles and polar angles for different conditions.

B. Graphs illustrating the polar angle differences and slope angle differences over time.

C. Graphs showing the tangential angle differences over time.

D. Graphs depicting the angular difference over time, with non-mirror and mirror onsets, and time of peak positive correction.
Figure 4

A Group M-VF subject

B Group M-KR subject

C Group C-KR subject

D Group N-KR subject

T1^{120}  T1^{90}  T1^{60}
Figure 5

A  Initial directional error, deg
B  Final positional error, cm
C  Reaction time, s

M-KR  M-VF
Figure 6

A Group M-VF subject

B Group M-KR subject

C Group C-KR subject

D Group N-KR subject
Figure 7

A. Group M-VF subject

B. Group M-KR subject

C. Group C-KR subject

D. Group N-KR subject

Time, s

Tangential angle, deg

Non-mirr. Base
Non-mirr. Test
Mirror

Base. T2^10
Base. T2^-10
Test T2^10
Test T2^-10

T1^{120}  T1^{90}  T1^{60}
Figure 8
Table 1
A. Experimental conditions per group and mean baseline performance.

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<td>PV, m s⁻¹</td>
<td>OC amplitude, °</td>
<td>RT, ms</td>
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<tr>
<td>Baseline</td>
<td>337 ± 76</td>
<td>.52 ± .07</td>
<td>T1⁶₀, T²+¹₀</td>
<td>14.0 ± 17</td>
</tr>
<tr>
<td>Test</td>
<td>425 ± 123</td>
<td>.49 ± .06</td>
<td>T1⁶₀, T²⁻¹₀</td>
<td>-12.7 ± 18</td>
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<tr>
<td>Baseline</td>
<td>329 ± 66</td>
<td>.50 ± .04</td>
<td>T1⁹₀, T²+¹₀</td>
<td>11.0 ± 19</td>
</tr>
<tr>
<td>Test</td>
<td>450 ± 110</td>
<td>.49 ± .06</td>
<td>T1⁹₀, T²⁻¹₀</td>
<td>-11.5 ± 15</td>
</tr>
<tr>
<td>Baseline</td>
<td>277 ± 40</td>
<td>.42 ± .06</td>
<td>T1¹²₀, T²+¹₀</td>
<td>13.7 ± 16</td>
</tr>
<tr>
<td>Test</td>
<td>357 ± 71</td>
<td>.49 ± .02</td>
<td>T1¹²₀, T²⁻¹₀</td>
<td>-14.9 ± 16</td>
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B. Results of repeated-measures ANOVA on reaction time and peak velocity.

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<th>Factors</th>
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<th>Peak velocity</th>
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<td>Group</td>
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<td>0.32</td>
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<td>Block</td>
<td>45.01</td>
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<tr>
<td>Block * Group</td>
<td>3.93</td>
<td>0.019*</td>
</tr>
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</table>

Effect of Group within each Block
- Baseline Block, group N-KR vs M-VF 3.87 0.002* 0.00 0.392
- Baseline Block, group N-KR vs M-KR 0.02 0.392 0.89 0.260
- Baseline Block, group M-KR vs M-VF 1.98 0.062 0.63 0.319
- Baseline Block, group M-KR vs C-KR 0.32 0.372 0.45 0.352
- Baseline Block, group M-VF vs C-KR 1.83 0.079 1.46 0.135
- Baseline Block, group N-KR vs C-KR 0.21 0.382 1.14 0.202
- Test Block, group N-KR vs M-VF 0.42 0.357 2.14 0.047
- Test Block, group N-KR vs M-KR 2.21 0.042 0.50 0.344
- Test Block, group M-KR vs M-VF 2.43 0.028 2.33 0.033
- Test Block, group M-KR vs C-KR 0.45 0.353 0.17 0.386
- Test Block, group M-VF vs C-KR 1.20 0.188 2.40 0.030
- Test Block, group N-KR vs C-KR 1.36 0.155 0.74 0.294

A. RT - reaction time; PV - peak velocity; OC - online correction. Values are means ± standard deviation. B. Significant α with Sidak correction for post-hoc analysis is 0.0085; * indicate significant p values.
**Table 2. Repeated-measures ANOVA on errors and reaction times during adaptation to the mirror transformation.**

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<thead>
<tr>
<th>Factors</th>
<th>Initial angular error</th>
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<th>Final positional error</th>
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<th>Reaction times</th>
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<td><strong>F</strong></td>
<td><strong>p</strong></td>
<td><strong>F</strong></td>
<td><strong>p</strong></td>
<td><strong>F</strong></td>
<td><strong>p</strong></td>
</tr>
<tr>
<td>Group</td>
<td>1.08</td>
<td>0.328</td>
<td>0.08</td>
<td>0.783</td>
<td>1.53</td>
<td>0.237</td>
</tr>
<tr>
<td>T1</td>
<td>0.65</td>
<td>0.485</td>
<td>3.35</td>
<td>0.080</td>
<td>2.58</td>
<td>0.130</td>
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<tr>
<td>T1 * Group</td>
<td>0.06</td>
<td>0.889</td>
<td>1.14</td>
<td>0.336</td>
<td>0.24</td>
<td>0.634</td>
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<tr>
<td>Bin</td>
<td>6.17</td>
<td>0.017*</td>
<td>4.60</td>
<td>0.043*</td>
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<tr>
<td>Bin * Group</td>
<td>3.56</td>
<td>0.066</td>
<td>1.56</td>
<td>0.246</td>
<td>1.11</td>
<td>0.356</td>
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<tr>
<td>T1 * Bin</td>
<td>2.50</td>
<td>0.052</td>
<td>2.07</td>
<td>0.119</td>
<td>2.52</td>
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<td>T1 * Group * Bin</td>
<td>1.67</td>
<td>0.171</td>
<td>0.81</td>
<td>0.513</td>
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**Effect of Group within each Bin**

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<tr>
<th>Bin</th>
<th><strong>F</strong></th>
<th><strong>p</strong></th>
<th><strong>F</strong></th>
<th><strong>p</strong></th>
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<tr>
<td>Bin 1</td>
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<td>1.75</td>
<td>0.091</td>
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<td>0.605</td>
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<tr>
<td>Bin 2</td>
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<td>0.362</td>
<td>0.75</td>
<td>0.457</td>
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<td>0.304</td>
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<tr>
<td>Bin 3</td>
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<td>0.385</td>
<td>0.96</td>
<td>0.344</td>
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<tr>
<td>Bin 4</td>
<td>0.60</td>
<td>0.553</td>
<td>0.03</td>
<td>0.972</td>
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<td>0.052</td>
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<tr>
<td>Bin 5</td>
<td>1.07</td>
<td>0.291</td>
<td>1.38</td>
<td>0.178</td>
<td>2.55</td>
<td>0.016</td>
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<tr>
<td>Bin 6</td>
<td>0.53</td>
<td>0.600</td>
<td>1.06</td>
<td>0.298</td>
<td>3.12</td>
<td>0.004*</td>
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</table>

Bin 1 - 6 indicate mean errors and reaction times per subject per T1 location averaged over consecutive 10-trials during the Adaptation block. Significant α with Sidak correction for post-hoc analysis is 0.006, * indicate significant p values. Post-hoc analysis included only the oblique T1 locations (T1^60° and T1^120°) to compare adaptation rates between groups. Trials with T1^90° target location caused very small errors and were excluded from post-hoc analysis.
Table 3. Repeated-measures ANOVA and post-hoc tests on onsets of trajectory deviations.

A. Main effects of the repeated-measures ANOVA

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<thead>
<tr>
<th>Factors</th>
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<tr>
<td>Group (between-subject factor)</td>
<td>1.29</td>
<td>0.302</td>
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<tr>
<td>T1 (within-subject factor)</td>
<td>0.75</td>
<td>0.440</td>
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<tr>
<td>T1 * Group (2-way interaction)</td>
<td>1.40</td>
<td>0.254</td>
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<tr>
<td>Condition (within-subject factor)</td>
<td>158.62</td>
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<tr>
<td>Condition * Group (2-way interaction)</td>
<td>1.11</td>
<td>0.374</td>
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<tr>
<td>T1 * Condition (2-way interaction)</td>
<td>0.39</td>
<td>0.783</td>
</tr>
<tr>
<td>T1 * Group * Condition (3-way interaction)</td>
<td>1.64</td>
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B. Effect of Condition factor (Baseline vs. Test block & mirror vs. non-mirror corrections) within Group and T1 factors

<table>
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<tr>
<th>Factors</th>
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<th>Onsets Levels 2/3</th>
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<td></td>
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<td>p</td>
<td>F</td>
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<tr>
<td>Group C-KR, T160</td>
<td>7.10</td>
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<td>4.08</td>
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<tr>
<td>Group C-KR, T190</td>
<td>3.58</td>
<td>0.004*</td>
<td>7.88</td>
</tr>
<tr>
<td>Group C-KR, T1120</td>
<td>6.15</td>
<td>0.000*</td>
<td>6.15</td>
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<tr>
<td>Group M-VF, T160</td>
<td>5.41</td>
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<td>Group M-VF, T190</td>
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<td>8.02</td>
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<td>Group M-VF, T1120</td>
<td>4.97</td>
<td>0.000*</td>
<td>2.71</td>
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<tr>
<td>Group M-KR, T160</td>
<td>4.53</td>
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<td>4.22</td>
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<td>4.86</td>
<td>0.000*</td>
<td>5.15</td>
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<tr>
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<td>Group N-KR, T1120</td>
<td>3.82</td>
<td>0.002*</td>
<td>5.26</td>
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Condition factor in ANOVA included 3 levels, which corresponded to non-mirror onsets in Baseline block (level 1), mirror onsets in Test block (level 2), and non-mirror onsets in Test block (level 3). Significant $\alpha$ with Sidak correction in B is 0.006; * indicate significant $p$ values.
Table 4. Repeated-measures ANOVA and post-hoc tests on amplitudes of trajectory deviations.

A. Main effects of the repeated-measures ANOVA

<table>
<thead>
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<th>Factors</th>
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<th>p</th>
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<td>0.000*</td>
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<tr>
<td><strong>T1</strong> (within-subject factor)</td>
<td>2.21</td>
<td>0.128</td>
</tr>
<tr>
<td><strong>T1 * Group</strong> (2-way interaction)</td>
<td>2.03</td>
<td>0.089</td>
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B. Effect of Group factor within Condition (Baseline and Test blocks) factor

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<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
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<tr>
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</tr>
<tr>
<td>Test</td>
<td>1.00</td>
<td>0.327</td>
<td>3.06</td>
<td>0.006*</td>
<td>1.09</td>
<td>0.288</td>
</tr>
</tbody>
</table>

C. Effect of Condition factor (Baseline vs. Test block) within Group and T1 factors

<table>
<thead>
<tr>
<th>Factors</th>
<th>T1&lt;sup&gt;60&lt;/sup&gt;: Baseline/Test</th>
<th>T1&lt;sup&gt;90&lt;/sup&gt;: Baseline/Test</th>
<th>T1&lt;sup&gt;120&lt;/sup&gt;: Baseline/Test</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group</strong></td>
<td>F</td>
<td>p</td>
<td>F</td>
</tr>
<tr>
<td>C-KR</td>
<td>23.68</td>
<td>0.000*</td>
<td>8.43</td>
</tr>
<tr>
<td>M-VF</td>
<td>29.64</td>
<td>0.000*</td>
<td>6.25</td>
</tr>
<tr>
<td>M-KR</td>
<td>18.29</td>
<td>0.000*</td>
<td>1.89</td>
</tr>
<tr>
<td>N-KR</td>
<td>0.74</td>
<td>0.48</td>
<td>2.93</td>
</tr>
</tbody>
</table>

D. Effect of T1 factor (between T1 locations) within Group and Condition (only Test block) factors

<table>
<thead>
<tr>
<th>Factors</th>
<th>Test: T1&lt;sup&gt;60&lt;/sup&gt;&amp;T1&lt;sup&gt;120&lt;/sup&gt;/T1&lt;sup&gt;90&lt;/sup&gt;</th>
<th>Test: T1&lt;sup&gt;60&lt;/sup&gt;/T1&lt;sup&gt;120&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group</strong></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>C-KR</td>
<td>1.31</td>
<td>0.164</td>
</tr>
<tr>
<td>M-VF</td>
<td>3.13</td>
<td>0.007*</td>
</tr>
<tr>
<td>M-KR</td>
<td>1.83</td>
<td>0.079</td>
</tr>
<tr>
<td>N-KR</td>
<td>1.29</td>
<td>0.168</td>
</tr>
</tbody>
</table>

ANOVA and most post-hoc tests (except Baseline in B) was done on amplitude values expressed as percentage of mean Baseline values, see Fig. 8B. Significant α with Sidak correction is 0.0085 in B, and 0.017 in C and D; * indicate significant p values; ¹ data not normalized to Baseline.