

Real-time error detection but not error correction drives automatic visuomotor adaptation

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Abstract We investigated the role of visual feedback of task performance in visuomotor adaptation. Participants produced novel two degrees of freedom movements (elbow flexion–extension, forearm pronation–supination) to move a cursor towards visual targets. Following trials with no rotation, participants were exposed to a 60° visuomotor rotation, before returning to the non-rotated condition. A colour cue on each trial permitted identification of the rotated/non-rotated contexts. Participants could not see their arm but received continuous and concurrent visual feedback (CF) of a cursor representing limb position *or* post-trial visual feedback (PF) representing the movement trajectory. Separate groups of participants who received CF were instructed that online modifications of their movements either were, or were not, permissible as a means of improving performance. Feedforward-mediated performance improvements occurred for both CF and PF groups in the rotated environment. Furthermore, for CF participants this adaptation occurred

regardless of whether feedback modifications of motor commands were permissible. Upon re-exposure to the non-rotated environment participants in the CF, *but not* PF, groups exhibited post-training aftereffects, manifested as greater angular deviations from a straight initial trajectory, with respect to the pre-rotation trials. Accordingly, the nature of the performance improvements that occurred was dependent upon the timing of the visual feedback of task performance. Continuous visual feedback of task performance *during* task execution appears critical in realising automatic visuomotor adaptation through a recalibration of the visuomotor mapping that transforms visual inputs into appropriate motor commands.

Keywords Visuomotor adaptation · Visual feedback · Sensory information · Motor learning · Contextual (colour) cues

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Introduction

The human motor system has a well-documented capacity to adapt to environments that are unlike any previously experienced. That is, behavioural changes ('adaptations') occur such that, with practice, performance in the novel environment will resemble that observed in the usual environment. This adaptation may be mediated by a variety of different neural and cognitive mechanisms. However, for any adaptation to occur a discrepancy between the task goal and the actual movement outcome (an error) must first be detected. The visual and somatosensory systems are the most important sources of such information and normally both systems are likely to contribute to error detection and, consequently, adaptation. In the case of mechanical perturbations, such as those imposed by torque motors (Shadmehr and Mussa-Ivaldi

1994; Caithness et al. 2004), errors occur because the limb is perturbed forcefully from its intended trajectory. This (trajectory) error can, in most situations, be detected by both the visual and proprioceptive systems. When this is the case, it has been suggested that the brain weights the estimate from each modality according to the preciseness or reliability of each estimate (Ernst and Banks 2002; van Beers et al. 1999, 2002). However, vision only (Ghez et al. 1995) or proprioceptive information only (Lackner and DiZio 1994; Tong et al. 2002; Scheidt et al. 2005; Franklin et al. 2008) can be sufficient for adaptation to occur. In the case of altered visuomotor environments, such as those imposed by prism goggles (e.g. Lackner 1974) or computer generated transformations (Flanagan and Rao 1995; Wolpert et al. 1995; Ghahramani and Wolpert 1997) or rotations (Cunningham 1989; Krakauer et al. 1999; Wigmore et al. 2002), error *is not* induced by a perturbation of the limb from its intended trajectory—participants plan and execute a movement as intended. Rather, the error signal occurs due to discordance between where participants sense they have moved to (via proprioceptive feedback), and where the manipulated (by way of computer-mediated transformation, for example) visual feedback indicates they have moved. Accordingly in these circumstances, the visual feedback of task performance is necessary to drive visuomotor adaptation. Indeed, in the absence of this visual feedback (and any other feedback of task performance relative to the intended goal, for example tactile information) participants would simply have no means to detect any performance error and, as such, there would be no impetus for adaptation.

Exposure to a novel (e.g. rotated) visual environment is usually characterised by initial large errors followed by incremental improvements in task performance. The latter phase is referred to as *visuomotor adaptation*. This adaptation is thought to occur as a result of an automatic recalibration of the original (i.e. appropriate for the non-rotated environment) internal model (Kawato 1999) that characterises the relationship between the coordinates of the visual environment (inputs) and the issued motor commands (outputs), such that it represents the altered visual environment (Cunningham 1989). This recalibration serves to reduce, and eventually remove, the discordance (error) between proprioceptive and visually derived feedback. Subsequent removal of the rotated environment typically leads to *aftereffects* (Krakauer et al. 1999; Wigmore et al. 2002), whereby trajectory errors in the opposite direction to those observed upon initial exposure to the rotated environment are observed. Aftereffects are indicative of motor commands that are generated on the basis of the newly acquired (i.e. recalibrated) visuomotor mapping. Re-adaptation to the non-rotated task (a reversal of the recalibration) is required for performance in the non-rotated task to return to baseline.

We previously reported that in an *isometric* task (Hinder et al. 2008) adaptation to a visuomotor rotation occurred in a manner that gave rise to the subsequent expression of aftereffects *only* when visual feedback of performance was provided *during* task execution, i.e., when the discordance between proprioceptive feedback and visual feedback could be detected as the action was unfolding. When visual feedback was provided *following* task execution, the rate and extent of the visuomotor adaptations were similar to those observed when visual feedback was provided during task execution. In these circumstances, however, aftereffects *were not* observed. The possibility that in the latter instance a cognitively mediated strategy was used to compensate for the imposed rotation was supported by the observation that reaction times were elevated during the adaptation phase.

It is conceivable, however, that the paucity of movement-related proprioceptive feedback that is an intrinsic characteristic of the isometric task resulted in forms of adaptation that were abnormally dependent on the nature of the visual feedback of task performance that was provided. To investigate this possibility, in the present study we employed a dynamic visuomotor adaptation task which recreated as closely as possible the isometric task (Hinder et al. 2008). Participants made two degree of freedom movements of the elbow–forearm complex in order to acquire visual targets. By its nature this task provides participants with proprioceptive feedback relating to changes of muscle force and limb position (muscle length), roughly analogous to that proprioceptive feedback available in everyday reaching tasks. In separate experimental conditions, visual feedback of task performance was available either during the movements (concurrently and continuously) or was provided following completion of each movement (terminal and discrete). It is apparent that provision of visual feedback during execution of a task permits online (or closed loop) error detection such that of motor commands can be modified to improve performance (i.e., adaptation). It is worth noting, however, that *perception* of the error is not necessary for adaptation (Pisella et al. 2000; Binsted et al. 2007; Klassen et al. 2005) Such online modifications are not possible when visual feedback of performance is provided following task execution, in which case the adaptation is necessarily based on a representation of the movement outcome. To determine if the implementation of such online modifications is a critical factor in determining the *nature* of visuomotor adaptation, we utilised two distinct concurrent (online) feedback conditions. In one, online modifications were permissible; in the other they were not. We hypothesised that both online and post-trial visual feedback of performance would enable performance improvements in the rotated environment, consistent with our previous work (Hinder et al. 2008).

However, we wished to test whether the manner in which adaptation occurred varied as a function of the type (online or post-trial) of visual feedback. An adaptation mediated by a recalibration of the visuomotor map would be expected to elicit aftereffects following training, while adaptation by way of a cognitive strategy would not be expected to elicit aftereffects. These ideas were tested using specific (pre-planned) statistical comparisons based on angular errors of movement trajectories.

Methods

Participants

Twenty-four self-reported right-handed participants (23–37 years) took part in this study. All participants gave informed consent to the procedures, which were approved by the Medical Ethics Committee of the University of Queensland, and conformed to the Declaration of Helsinki.

Apparatus

Participants sat in a height-adjustable chair 1 m from a computer screen, positioned at eye level. The dominant right arm was placed in a manipulandum that allowed movement in two degrees of freedom (d.f.): elbow flexion/extension

and forearm pronation/supination. The back of upper arm was placed against a vertical padded brace and held stationary, adjacent to the torso, by a Velcro strap. Participants grasped an instrumented vertical cylindrical handle, with pads positioned above and below in order to minimise movement of the hand. The chair height was adjusted for each participant such that the upper arm was aligned vertically and the centre of rotation of the elbow and the centre of rotation of the flexion/extension axis of the manipulandum were coincident (Fig. 1; see Shemmell et al. 2005 for further details). This task represented the dynamic equivalent of the isometric task reported in our previous work (Hinder et al. 2008). As such, any change in the manner of the observed adaptation could be assumed to be as a result of a change in the nature of the proprioceptive feedback.

Potentiometers coupled to each axis of the manipulandum enabled real-time feedback of the angular position of the limb (flexion/extension and pronation/supination). These kinematic recordings were sampled at 2,000 Hz at an analogue to digital interface (AT-mio-16E-10, National Instruments, TX, USA) and stored on a personal computer for further offline analysis. Labview (vers 5.0, National Instruments, TX, USA) was used to write experimental control and data acquisition programs.

A vertical cloth screen was carefully positioned between the participants' torso and arm, such that they were unable to see their arm, or the manipulandum itself, throughout the

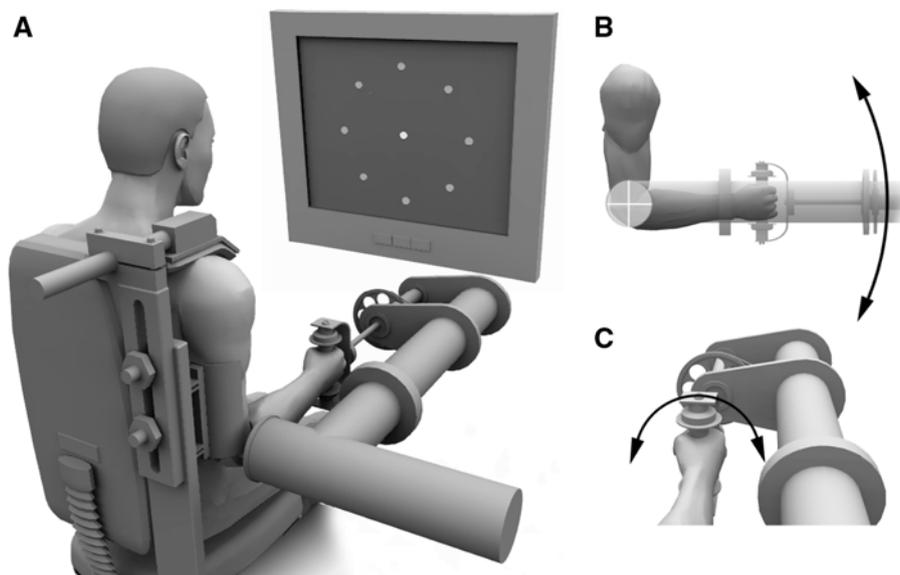


Fig. 1 Experimental set-up. **a** Apparatus. Participants held the manipulandum and controlled a visual cursor displayed on the screen via flexion–extension (up–down cursor movement) and pronation–supination (left–right cursor movement) movements of the elbow–forearm complex (see **b** and **c**, respectively). Torque was applied to the servo-controlled motor controlling the flexion–extension axis such

that when participants relaxed their arm (with the upper arm against the restraint), their forearm was horizontal and the cursor appeared at the start position in the centre of the screen (depicted as a *white dot*). One of eight visual targets (represented as *grey dots*), equally spaced around the start position, was presented on each trial

experiment. Consequently, participants had to rely upon the visual feedback provided on the computer screen and proprioceptive/kinaesthetic feedback. By perturbing the visual feedback by way of a visuomotor rotation (see “[Experimental paradigm](#)”), we were able to introduce discordance between the position of the limb as indicated by the proprioceptive and visual sensory modalities.

Task procedure

A yellow dot at the centre of the screen, representing the start zone (zero displacement), was presented at the beginning of each trial. A white cursor indicated the current location of arm (in each degree of freedom). A gravity-compensation torque was applied via a servo-controlled motor (Brushless Servo Motor; Baldor Electric Co.) in the flexion–extension degree of freedom, to compensate for the gravitational effects corresponding to the combined weight of the manipulandum and the participant’s arm.¹ As such, when each participant relaxed their arm (with the upper arm secured against the padded restraint, their forearm was horizontal and the cursor appeared at the start position in the centre of the screen (Fig. 1). In the pre-movement period (i.e., before presentation of the target in each trial) the white cursor representing current arm position was only visible when the arm remained within the start zone (forearm horizontal; palm vertical, i.e., midway between pronation and supination; $\pm 3.6^\circ$). The visual feedback around the start position allowed participants to make small positional adjustments to ensure they were in the start position, but precluded them from investigating the arm movement–cursor movement relationship over the wider workspace. The visual display (active screen area) was an 18 cm square region, on which the visual cursor moved 1.5 cm for every 10° of joint rotation in either d.f. As such, 60° of pronation/supination or flexion/extension from the central start position would result in the cursor being displaced to the limits of the visual display.

Each trial began with a period of random duration (1–2 s) during which participants were instructed to stay relaxed with the cursor in the start zone. One of eight targets, equally spaced at 45° intervals around, and at a constant distance of 5.4 cm from the start zone, was presented, accompanied by an auditory tone. Each target represented a resultant joint rotation of 36° . For single d.f. targets, a rotation of 36° in a single direction was required. For targets representing rotations in both d.f., the vertical (flexion/extension) and horizontal (pronation/supination) requirements of the target were determined as the cosine of the subtended angle

between the target direction and the single degree of freedom target (45°), multiplied by the joint rotation/target displacement for a single degree of freedom target. Accordingly, the 2 d.f. targets required 18° rotation in each degree of freedom. Participants were instructed to react quickly upon presentation of the target, and move the cursor towards the target as quickly as possible by moving their arm in one or both d.f.

The servo-control motors applied forces in proportion to the angular displacement in each degree of freedom (i.e., stiffness forces with an equilibrium position that coincided with the start position for each trial). For the vertical (flexion–extension d.f., this torque was imposed over-and-above the gravity-compensation torque described above). The magnitude of the resistive force (controlled by K in the equation $\tau = -K\theta$, where τ is the imposed torque and θ is the angular displacement of the limb) did not vary between participants and experimental blocks (see “[Experimental paradigm](#)”). Pilot testing had revealed that participants could acquire the targets in each trial without considerable physical effort. Participants did not report the experiment to be physically fatiguing.

Experimental groups

Participants were randomly assigned to one of three groups ($n = 8$ per group). These groups undertook the experiment with varying types of visual feedback of task performance. Two groups were presented with continuous visual feedback of the cursor position over the whole workspace during the trial (i.e., concurrent feedback, CF), while the third group was provided with post-trial feedback (PF) following task execution (Table 1).

The PF group and one of the CF groups were instructed to react quickly upon presentation of each target and generate a single fast, *un-corrected*, arm movement to move the cursor from the start position toward the target. Participants subsequently relaxed such that their arm and the cursor returned to the starting position (elbow at 90° ; forearm in a neutral position) in preparation for the next trial. Thus, for these groups, we assessed task performance in the absence of intended online modifications.

The PF group were unable to see the cursor representing their position with respect to the visual target during each movement. Rather, they were presented with knowledge of performance (KP) depicting the cursor path, from movement onset (see “[Data Reduction and Analysis](#)”) to final position following task execution. As such, this group will be referred to as the PF–KP group. Final position (i.e., movement offset) was defined as the screen position corresponding to the flexion–extension (y-component) and pronation–supination (x-component) components of the maximum resultant joint rotation. Following the

¹ This torque was determined for each participant on an individual basis to account for differences in the weight and length of participants’ arms.

Table 1 Task instructions and visual feedback conditions for the three participant groups

Group	Paradigm/number of trials	Visual feedback	Task
CF–FF	PRE (black screen): 10 per target = 80 ROT (blue screen): 40 per target = 320 POST (black screen): 10 per target = 80 480 total trials	Continuous, concurrent	React quickly and move cursor towards target—do not make corrections
CF–FB	PRE (black screen): 10 per target = 80 ROT (blue screen): 40 per target = 320 POST (black screen): 10 per target = 80 480 total trials	Continuous, concurrent	React quickly and make any necessary corrections to acquire target
PF–KP	PRE (black screen): 10 per target = 80 ROT (blue screen): 40 per target = 320 POST (black screen): 10 per target = 80 480 total trials	Post-trial feedback of cursor path (KP)	React quickly such that post-trial feedback shows path terminating near target- do not make corrections

movement, PF–KP participants relaxed, such that their arm returned to the start position, where they waited for the feedback of their performance, which was presented 5 s after the trial began for a period of 3 s. Following this feedback period, the next trial began. Therefore, there was an 8 s interval between the onsets of the fore-periods in consecutive trials.

Participants in the first CF group were instructed *not* to make any online (feedback mediated) corrections to their movements despite being able to see the cursor representing arm position throughout the task. Accordingly, this group will be referred to as the continuous feedback, feedforward control group (CF–FF). For this group, the fore-period of consecutive trials began at 8 s intervals, as per the PF–KP group.

The second CF group were instructed to react quickly when the target was presented, move towards *and* make whatever online corrections necessary in order to ensure that the target was acquired in each trial (i.e. it was a requirement for “success” that the cursor representing the magnitude and direction of movement in each d.f. in each trial coincided with the target zone for at least 100 ms). This variant of the task promoted *online* (visual feedback mediated) corrections. Therefore, this group is referred to as the concurrent visual feedback with feedback correction group (CF–FB). The purpose of this group was to determine if executing feedback modifications facilitated feedforward adaptation compared to the condition where concurrent visual information was provided, but feedback modifications were not promoted.

For the CF–FB group, when the cursor was held within the target zone, defined as a region $\pm 5\%$ around the specific visual target (representing a resultant joint displacement of 36° from the starting position, $\pm 1.8^\circ$) for 100 ms a second auditory tone sounded, at which point participants relaxed and their arm (and cursor) returned to the start position. For this group, movement offset was defined as

the point 100 ms before the second tone. Pilot testing revealed that to provide CF–FB participants with sufficient time to make online corrections to acquire the target a slightly longer trial duration was required. This was especially true in the first few trials in the rotated task (see below for [Experimental paradigm](#)). Consecutive trials began at 9 s intervals. Although the *rate* at which trials were conducted in the CF–FB group was slightly slower than the other two groups, the longer movement times for the CF–FB group ensured that the time periods between completion of the task in one trial and commencement of the subsequent trial was very similar across all participant groups.

Experimental paradigm

All groups undertook a short practice block of trials (four trials per target), in which online feedback of the cursor position *was* available. The relationship between movement of the forearm and movement of the cursor was non-rotated: elbow flexion and extension movement resulted in vertically upward, and downward, cursor movement, respectively. Pronation and supination movement resulted in cursor movement to the left, and right, respectively. Within each group of 16 trials, two trials to each target were undertaken; the order of target presentation within this ‘cycle’ was pseudo-randomised. The practice block consisted of two such cycles. Despite provision of online feedback in this short pre-experimental block, PF–KP and CF–FF participants were instructed to make one rapid, uncorrected cursor movement towards the target—as per the instructions for the subsequent experimental blocks (see below). CF–FB participants made trajectory modifications as required, in order to acquire the presented target. The purpose of this block was threefold. Firstly, it ensured that all participants understood how to produce movements in each orthogonal d.f. Secondly, it enabled participants to

appreciate the magnitude of the joint rotations (movements) required to move to the vicinity of the target. This would ensure that in subsequent blocks for the PF–KP group the position of the cursor relating to maximum movement amplitude was not beyond the limits of the visual display. Moreover, it prevented all participants from making gross over-rotations in either degree of freedom such that the manipulandum approached its' working range.²

Finally, these trials taught the CF–FF group to resist any urge they had to produce corrective movements on the basis of the visual information that was available to them. These practice trials were not included in any statistical analysis.

All groups subsequently undertook three experimental blocks of trials. All trials in a given block were conducted in the presence of a specific relationship between the direction of movement and the direction of the ensuing cursor movement. The background colour of the display, during both the trial and in the post-trial feedback period (for the PF–KP group), indicated the operative relationship between the direction of movement and the resulting displacement of the cursor. The PRE block (10 trials to each target; 5 cycles; 80 trials total) was undertaken without any rotation imposed on the elbow movement–cursor movement mapping i.e., the conditions were identical to those experienced in the short practice session. PRE trials were conducted with a black background. Participants could therefore associate this arm movement–cursor movement relationship with the contextual cue (screen colour).

Following the PRE block, participants were exposed to a block of trials in which the feedback of cursor position was rotated 60° clockwise (CW) with respect to the direction of elbow movement (ROT block). By convention, this rotation was assigned a negative direction (−60°). This block consisted of 40 trials to each target (20 cycles, 320 trials total). The vertical and horizontal target requirements were re-calculated according to the imposed 60° CW rotation, such that the resultant joint rotation required to acquire each target remained at 36°. All ROT trials were performed with a blue background throughout the trial and, for the PF–KP group, during the post-trial feedback periods. Participants were thus provided with the facility to associate the novel arm movement–cursor movement relationship

with the blue screen. Finally, participants were re-exposed to the original (non-rotated) mapping which they had previously encountered in the PRE block (POST block). A black screen was used, as in the PRE block, allowing the restoration of the original (non-rotated) visuomotor relationship to be identified. The purpose of the POST block was to probe for aftereffects that may have occurred as a result of exposure to the rotation. The group-specific visual conditions, and task instructions, discussed above were relevant in each of the three experimental blocks for each group. The PF–KP group received only post-trial feedback in each block). The presentation of targets within each cycle was pseudo-randomised such that each participant within a group was presented with a different target on the first trial of each trial block.

In total, the experimental protocol lasted ~75 min. There was a brief break (<1 min) between consecutive blocks of trials in which participants remained seated with their arm relaxed. All participants were explicitly reminded at the start of the each experimental block to react quickly upon presentation of each target, and that the relationship between their movement and movement of the cursor in all trials was represented by the colour of the screen. As such, participants had sufficient information to enable them to identify the non-rotated environment at the commencement of the POST block.

Data reduction and analysis

Movement time series, representing cursor position in the two orthogonal degrees of freedom (flexion–extension and pronation–supination of the forearm–elbow complex), were digitally low-pass filtered at 15 Hz with a second-order, dual-pass Butterworth filter. Movement onset was determined using an algorithm based on cursor speed (Teasdale et al. 1993), with an initial threshold of 15% of the maximum tangential speed. For the CF–FB group, movement offset was determined as the time 100 ms prior to the second tone, i.e., the start of the first period of at least 100 ms duration in each trial in which subjects remained in the target zone. For the CF–FF and PF–KP groups, movement offset was determined as the point of maximum resultant joint rotation.

Movement time, MT, from movement onset to movement offset, i.e., target acquisition (CF–FB group) or maximum resultant joint rotation (other groups), was used to assess performance within groups. This measure was *not* used as the basis of comparison between groups as extra time was required by CF–FB participants to issue corrective motor commands to acquire the target. For the groups who were instructed not to make feedback modifications, we predicted that MT would be unaffected by imposition of the rotation. For the CF–FB group, however, longer MTs

² As a precaution to help prevent this scenario, the servo-motors controlling movement in each degree of freedom were programmed with elastic 'walls' at the limits of the visual display, i.e., very large torques were required to move beyond a 60° rotation from the start position. If the manipulandum approached these limits, participants would feel a strong spring-like force that repelled them away from region corresponding to the edge of the visual display. We note, however, that no participants hit the 'walls' within the experimental trials.

would be predicted upon initial exposure to the rotation due to increased requirements for feedback modifications to acquire the target. Reductions in MT during the course of each block (PRE, ROT, POST) would be expected for two reasons: firstly, progressively more accurate feedforward commands would result in smaller feedback corrections being required, and secondly with practice participants should be able to implement the required feedback corrections more quickly.

Angular error, θ , was calculated at two points within the trial: 100 ms after movement onset, and at the peak resultant velocity (i.e., the peak resultant velocity of the arm). We calculated the average angle between the vector defined by the start and target positions, and the vector defined by the start position and actual cursor position, in a 10 ms window centred at either 100 ms after movement onset or peak resultant velocity, respectively. On the basis of the assumption that no responses based on the online visual feedback provided to the CF–FB group could occur prior to 100 ms, this measure assessed *feedforward* performance. The angle at peak resultant velocity was calculated to take account of differences in movement times between participant groups (see “Results”) i.e., 100 ms following movement onset represented a different position in the trial, with regard to acceleration and deceleration phases. Hand path characteristics up to peak resultant velocity are generally accepted as being independent of online corrections, i.e., representative of feedforward performance.

We predicted that increased angular errors would occur for all groups due to imposition of the rotation. Reduction of angular error within the training (ROT) block would signify compensation for the rotation. Angular errors in the POST block that were in the opposite direction to those exhibited upon initial exposure to the rotation (aftereffects) would indicate that participants implemented motor commands more appropriate for the rotated context. However, accurate performance in the POST block would indicate that participants correctly implemented commands for the non-rotated task.

Reaction time, RT, was calculated as the interval from target presentation to movement onset, to assess the extent of pre-movement processing. Adaptation to the rotation through mechanisms that amended the visuomotor map (i.e., implicit adaptation, Mazzoni and Krakauer 2006) would not be expected to result in increased reaction times. If, however, participants adapted in a manner that required explicit decisions or compensation strategies to be implemented, planning time may increase and result in longer RT.

We determined cycle-average (over the 16 trials of each cycle; two trials to each target location) data for the five cycles of the PRE and POST block, and the 20 cycles of the

ROT block for each participant group for each dependent variable (θ , RT and MT). The values for the first and last cycle of each movement block (PREinitial, PREfinal, ROTinitial, ROTfinal, POSTinitial and POSTfinal) were used to conduct statistical comparisons of performance (averaged across all target conditions) for each dependent variable. Assessing performance based on cycle-averages is common within the motor learning literature (e.g. Krakauer et al. 1999; Caithness et al. 2004) as it allows one to assess performance in a manner that is representative of movements to *all* targets, rather than just a single target.

A three-way (group {CF–FB, CF–FF, PF–KP} \times block {PRE, ROT, POST} \times time {initial, final}), ANOVA with repeated measures on the final two factors was conducted for each dependent variable. However, in the context of the present experimental design, the majority of the main effect and interaction terms associated with the ANOVA are of no real benefit in aiding with the interpretation of the results. The purpose of the ANOVA was to compute the values (i.e. sums of squares, etc.) that enabled us to undertake *planned comparisons*. Because the comparisons we report were all planned, they can be reported in the absence of significant main effect or interaction terms (c.f. post hoc tests, where main or interaction effects must be significant to allow post hoc analyses; see Keppel 1982). PREinitial was compared with PREfinal to assess any performance changes within the non-rotated (pre-training) block, while comparing ROTinitial with ROTfinal enabled us to determine if there was a significant performance improvement within the rotated environment. POSTinitial was compared with PREfinal to determine any changes in performance in the non-rotated condition as a result of exposure to the rotation block, i.e., to probe for aftereffects as a result of exposure to the rotated environment. This particular comparison provides a robust test for aftereffects, because it is independent of the degree of adaptation during training. A final comparison of POSTinitial with POSTfinal assessed whether there were any reliable changes in performance over the course of the POST block. Adjustments to alpha (modified Bonferroni adjustment) were made as necessary to account for multiple comparisons. Effect sizes, f , were calculated for each of the planned comparisons (Cohen 1969), to aid in the interpretation of the tests of significance. The effect size describes the degree of departure from no effect, in other words, the degree to which the phenomenon is manifested.

The rate of performance improvements (reduction in angular error) in the rotated environment were compared across groups by fitting a power function to the cycle-averaged trial data in the training (ROT) block for each participant, using a least-squares fit criteria (Newell and Rosenbloom 1981). This function takes the form

$$y = ax^b$$

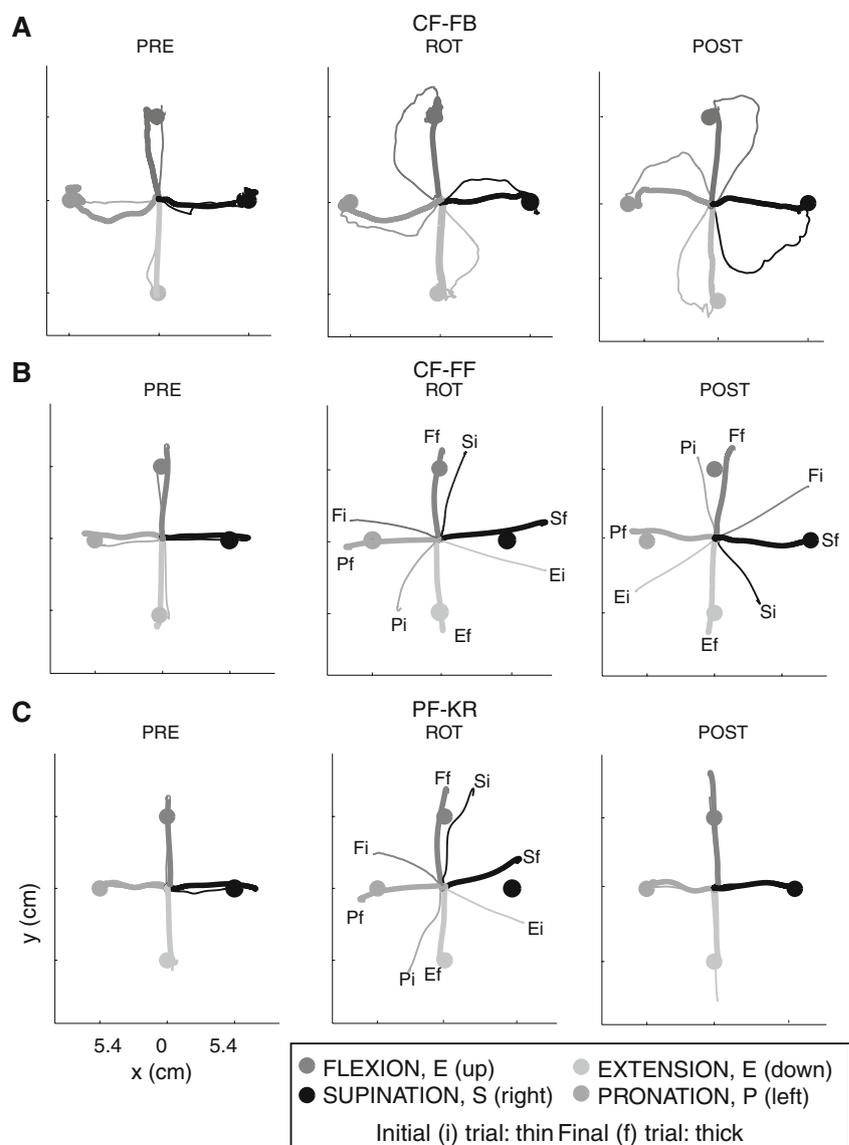
where y represents the angular error in cycle x , a indicates the (fitted) level of performance in the first cycle in the rotated environment and b represents the slope of the curve, and is an indication of the rate of adaptation. While fitting curves to the *cycle-average* data is consistent with our use of cycle-averages to determine the initial and final performance in the rotated context (c.f. Caithness et al. 2004; Krakauer et al. 1999), the curve parameters may not be sufficiently sensitive to detect subtle differences in the adaptation rates which may appear when considering *individual trials*. Accordingly, we also fitted curves to the individual trial data for each participant (in this instance y represents the error in trial x). One-way ANOVA was used to compare adaptation rates (b parameter from the curve

fitting procedure) for the three feedback groups, for each of the two fitting methods independently.

Results

Figure 2 shows cursor trajectories in the PRE, ROT and POST blocks for a representative participant from each group. Each participant produced relatively straight paths in the PRE block (left panels). In the initial ROT trials (central panels; thin traces), all groups exhibited large angular errors early in the movements as a result of the imposed rotation. The CF–FB group exhibited large ‘hooks’ in the trajectory indicating online corrections such that the target was attained (Fig. 2a; thin traces). In contrast, the other groups exhibited angular errors at the

Fig. 2 Example cursor paths. Paths are shown for the first (thin line) and final (thick line) trial in each block (PRE, left; ROT, centre; POST, right) to the flexion (top), extension (bottom), pronation (left) and supination (right) targets for the **a** CF–FB **b** CF–FF and **c** PF–KR groups. For the CF–FB group, online corrections ensured that all paths terminated at the desired target. However, terminal errors remained for the other groups as online corrections were not permitted (When required, these trajectories are labelled to ensure it is clear to which target the participant was aiming—see key). All groups exhibited performance improvements within the training (ROT) block; however, *only* the groups who received online visual feedback exhibited aftereffects when the rotation was removed (POST block). Data shown are individual trials of a single participant in each of the experimental groups



movement endpoint similar to the errors observed earlier during the movement, suggesting that corrective movements were not made (Fig. 2b, c; thin traces). All groups had significantly straightened hand paths in the initial part of each movement by completion of the ROT block (Fig. 2; central panels, bold traces). However, *only* the groups provided with continuous visual feedback exhibited after-effects when the rotation was removed (Fig. 2a, b; right panels, thin traces); the post-trial feedback group manifested paths straight towards the targets (Fig. 2c; right panel, thin traces), resembling those observed immediately prior to the rotation.

To corroborate that the CF–FF and PF–KP groups adhered to the task instructions and did not make corrective movements we calculated the time derivative of individual movement profiles. After applying a low-pass (6 Hz Butterworth) filter to remove noise associated with the differentiation process, we calculated the number of peaks in these velocity profiles and determined the mean number of velocity peaks for each 16-trial cycle of the ROT block (Fig. 3). Two-way ANOVA revealed a significant group effect ($p < 0.001$, $\eta_p^2 = 0.88$) indicating that the number of velocity peaks varied between groups. Subsequent pairwise comparisons indicated that the CF–FB group

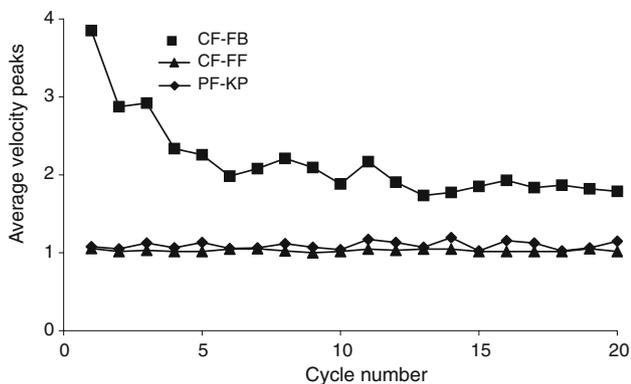


Fig. 3 Average number of peaks in the velocity profile. Data shown is the group-average for each cycle in the ROT block (CF–FB squares; CF–FF triangles; PF–KP diamond; also see key)

exhibited a higher number of corrections than either of the other two groups ($p < 0.001$ in both cases) but that the number of corrections in the PF–KP and CF–FF groups did not differ significantly ($p > 0.99$). The cycle-number main effect was also significant ($p < 0.001$, $\eta_p^2 = 0.42$) indicating that, averaged over the three groups, the number of corrective movements fell with training. However, the interaction between cycle-number and group was also significant ($p < 0.001$, $\eta_p^2 = 0.59$). This interaction, together with visual inspection of Fig. 3, clearly indicates that the cycle main effect was driven solely by the reduction in the number of velocity peaks across repeated cycles by the CF–FB group. In contrast the other two groups had a low (~ 1) number of velocity peaks throughout the training period. This result indicates that both the CF–FF and PF–KP groups adhered to instructions and did not make corrections to their movements during each trial.

Figure 4 shows angular error (measured at peak resultant velocity, see “Data reduction and analysis” and “Angular error”) in each trial of the PRE, ROT and POST blocks, averaged over the 8 participants in each groups. Figure 5a–b shows cycle-averaged data (for angular errors and movement times) derived from the individual trial data in Fig. 5.

The cycle-average data presented in Fig. 5 indicate (qualitatively) that throughout the PRE block, when averaged over the eight targets, participants produced movements that resulted in relatively accurate movement of the cursor towards the target (Fig. 5a, PRE block cycles). The low magnitude of θ throughout the PRE block, together with low variability of error between the cycles of the PRE block indicates that participants found the arm movement–cursor movement mapping fairly intuitive (i.e., there is no trend in the angular errors within the PRE block to indicate that any adaptation occurred with respect to movement direction/control). We note that small angular errors were observed throughout the short practice block (data not shown), suggesting that the low errors in the PRE block were a result of participants finding the non-rotated visuomotor mapping intuitive, rather than a result of rapid adaptation in the practice block. Exposure to the 60° CW

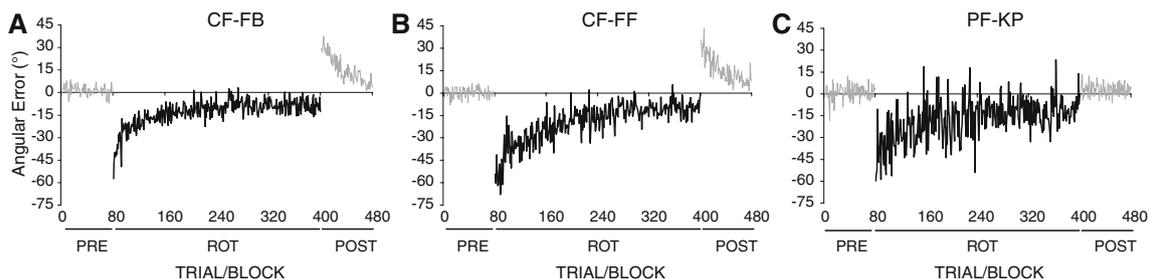


Fig. 4 Angular errors measured at peak joint velocity- individual trial data. Data shown is the group-average for each trial of the PRE, ROT and POST blocks for the **a** continuous feedback with online

corrections CF–FB **b** continuous feedback with no online corrections CF–FF and **c** post-trial feedback PF–KP groups

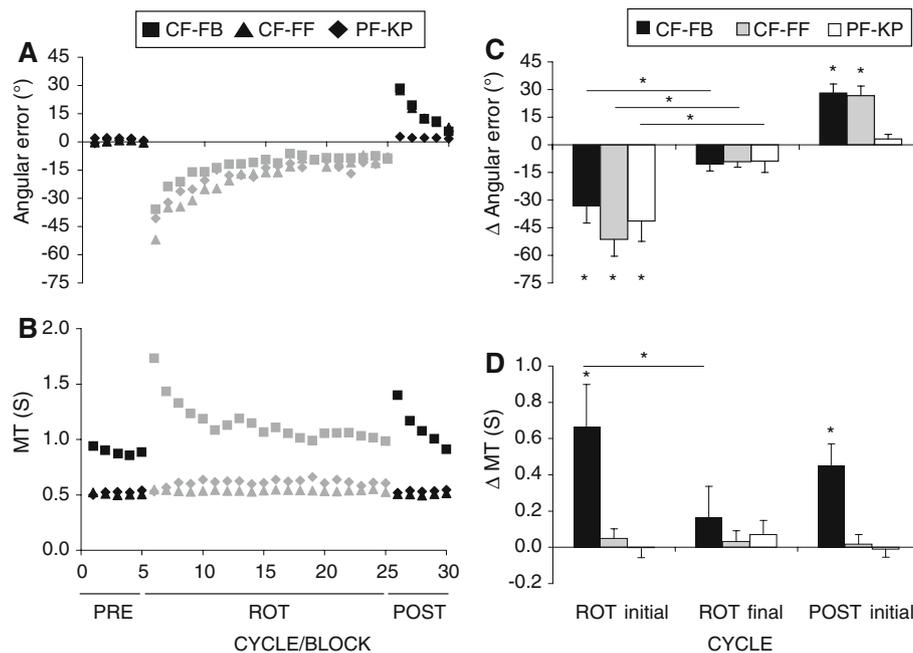


Fig. 5 Cycle-average angular errors and movement times. Data is shown for the PRE, ROT and POST blocks, averaged across the eight participants in each group (CF–FB squares; CF–FF triangles; PF–KP diamonds; also see key). **a** Angular error and **b** Movement time. Note that in **b** the data for the CF–FB and CF–FF groups are coincident in the POST block cycles (i.e., the triangles are predominantly hidden behind the squares). For all groups, the PRE and POST block data are presented as black symbols, while the ROT block data appears as grey

symbols. **c–d** Mean ($\pm 95\%$ confidence intervals) difference (Δ) in angular error (**c**) and movement time (**d**) in the ROTinitial, ROTfinal and POSTinitial cycles, relative to the PREfinal cycle. A asterisk above the ROTinitial or POSTinitial bars indicates a significant change relative to the corresponding PREfinal value ($p < 0.05$). Significant changes between ROTinitial and ROTfinal are depicted by horizontal lines and asterisk

rotation resulted in angular errors, observable in the direction of the rotation (i.e., negative errors by convention) for all groups (Fig. 5a, ROT block). The fact the magnitude of the errors were somewhat less than the imposed rotation of 60° indicates that a certain degree of adaptation occurred within the first cycle of trials, a characteristic that can be observed in Fig. 4. With repeated exposure to the rotation, all groups were able to reduce the angular errors in the initial period of the movement, indicating modification of the feedforward motor commands (Fig. 5a, final ROT cycles). Following completion of the training (ROT) block, performance with respect to angular error was similar across the three participant groups, and was of the order of -10° (i.e., participants did not quite compensate fully for the imposed rotation of -60°). We note that the CF–FB group, who were instructed to make corrections to movements within each trial, were able to accurately acquire the targets on the vast majority of trials, i.e., despite exhibiting angular errors at peak velocity comparable to the other groups, they reduced these errors in the deceleration phase of the movement, and located the target (to within $\pm 5\%$ of the specified target joint rotations; see “Methods”)

For the both the CF–FF and CF–FB groups, re-exposure to the non-rotated environment (POST block) resulted in

angular errors in the opposite direction to those errors observed when they had first encountered the rotation (Fig. 5a, initial POST block cycles, squares and triangles), i.e., aftereffects were observed. By the end of the POST block, paths had become significantly straighter for both CF groups. In contrast, the PF–KP group implemented motor commands (i.e., generated arm movements) in the initial POST block trials that resulted in cursor movements that were accurately directed towards the targets (Fig. 5a initial POST cycles, diamonds), i.e., no aftereffects were apparent. The presence of aftereffects for the continuous feedback groups, together with the absence of aftereffects for the post-trial feedback group is also clear in Fig. 4. Thus, although all groups appeared to be able to improve feedforward performance similarly in the rotated environment, only the CF groups’ performance in the non-rotated environment was affected as a consequence.

Figure 5c–d depicts the angular errors and movement times in the ROTinitial, ROTfinal and POSTinitial positions, relative to the value of the corresponding PREfinal value. These panels allow the reader to clearly see the how each dependent variable varied within the training block, and upon re-exposure to the non-rotated task, with respect to the value of the variable following completion of the PRE block. Statistical analyses (pre-planned comparisons as indicated in “Data

Reduction and Analysis”) were performed on the cycle-average data for the first and last cycle of each movement block for each dependent variable. These are reported below.

Angular error

We investigated *feedforward* performance by considering angular deviations of the cursor path at peak velocity, i.e., before any corrective movements would have occurred for the CF–FB group. We note that the time at which peak velocity occurred (265–328 ms following movement onset) did not vary significantly across the three groups (one-way ANOVA, $p > 0.20$; $f = 0.10$).

Initial exposure to the rotation (ROTinitial) led to an increase in θ relative to the PREfinal cycle for all groups ($p < 0.05$ for all groups; $f = 0.77, 1.20, 0.97$ for the CF–FB, CF–FF and PF–KP groups, respectively). By completion of the training (ROTfinal), all groups performed more accurately than they had upon initial exposure to the rotated task context ($p < 0.05$; $f = 0.53, 0.99, 0.77$ for CF–FB, CF–FF and PF–KP, respectively). Aftereffects as a result of exposure to the rotated environment were assessed by comparing θ in the cycle immediately prior to (PREfinal) and following (POSTinitial) the rotation block. For both CF groups this comparison was statistically significant ($p < 0.05$) and was associated with a large effect size ($f = 0.66, 0.62$ for the CF–FB and CF–FF groups), indicating the presence of aftereffects. In contrast, for the PF–KP group this comparison was *not* statistically significant ($p = 0.49$), was associated with a small effect size ($f = 0.07$) and suggests that *no* aftereffects were present for this group.

Inter-group comparisons of final performance

A one-way ANOVA indicated that the angular error in the final ROT cycle, (i.e., upon completion of the training period) did not differ significantly across the three groups ($p = 0.77$; $f = 0.16$). Furthermore, we also determined that the co-efficient of variation of angular error (measured at peak velocity) within the 16 trials of the final training (ROT) cycle did not vary as a function of group (One-way ANOVA, $p = 0.38$, $f = 0.14$). As such, following training, both performance and performance variability were comparable across groups. Accordingly, the presence of aftereffects for the CF groups, and absence of aftereffects for the PF–KP group (reported above) *cannot* be attributed to inter-group differences in the level of skill acquired during the training epoch or the variability of performance.

Individual trial analysis

While cycle-averaging is a common technique enabling performance to be assessed across all target directions, it is

conceivable that such a process could mask subtle changes in performance that were present in the first few trials of a cycle. Specifically, we wished to ensure that cycle-averaging did not conceal any post-training aftereffects for the PF–KP group which were quickly reduced (re-adaptation in the non-rotated environment) and as such not apparent in the POSTinitial cycle.

Linear regression was conducted on the 16 individual trials of the POSTinitial cycle. For the PF–KP group, the gradient of the regression was not significantly different to zero ($p = 0.83$), indicating there was no significant trend in angular error within the 16 trials of the first cycle in the POST block. Furthermore, the intercept parameter of the regression was not significantly different to zero ($p = 0.16$). Indeed, the PF–KP group-average angular error in the very first POST trial was 1.3° . This suggests that aftereffects were not manifested by this group, even in the very early POST block trials. For both CF groups the gradient of the linear regression was less than zero, although this did not reach significance for the CF–FB group ($p = 0.10$ for CF–FB; $p < 0.05$ for CF–FF). Moreover, the intercept parameters of the regressions for these groups were both significantly greater than zero ($p < 0.05$), indicating significant aftereffects. These results suggest the substantial aftereffects exhibited by the CF groups were incrementally reduced (to some degree) over the course of the 16 trials of the first cycle (as supported by Fig. 4).

Overall, the angular error results suggest that the ability to issue appropriate motor commands when re-exposed to the non-rotated environment following exposure to an altered visual environment varied as a function of the visual feedback of task performance (concurrent or post-trial) that was provided.

Comparisons of adaptation rates

Power fits were derived from the angular error data using both cycle-average data and individual trials (see [Methods](#)). In all cases, the fits were statistically reliable ($p < 0.05$) such that the parameters derived could be assumed to be a true representation of the dynamics of the adaptation process.

Cycle-average fits

Average r^2 values for these fits were 0.37, 0.65 and 0.66 for PF–KP; CF–FF; and for CF–FB groups, respectively. One-way ANOVA failed to show any significant differences in the adaptation rates across the three groups ($p = 0.51$; b parameter = $-0.47, -0.61, -0.55$ for the PF–KP, CF–FF and CF–FB groups, respectively) suggesting that despite differences in the visual feedback and task

instructions, participants were able to reduce error at the same rate within the training period.

Individual trial fits

To assess subtle differences in the adaptation rates that may have been obscured as a result of cycle-averaging, we fitted power functions to the individual trial data for each individual subject. While the r^2 values (average 0.10, 0.18 and 0.24 for PF–KP, CF–FF and CF–FB groups, respectively) were lower than r^2 values for those fits derived from cycle-average data, the fits were still reliable ($p < 0.05$). One-way ANOVA indicated that, in contrast to the cycle-average analysis, there was a statistically reliable difference in the adaptation rates (b parameter) between the three groups ($p < 0.005$; $b = -0.10, -0.17, -0.18$ for the PF–KP, CF–FF and CF–FB groups, respectively). Subsequent post hoc analyses indicated that the adaptation rates for the two groups provided with continuous visual feedback were not dissimilar ($p = 0.66$), but that the post-trial feedback group appeared to adapt more slowly than both continuous feedback groups ($p < 0.05$).

Movement time: a measure of overall task performance

MTs varied little between and within blocks for the CF–FF and PF–KP groups (Fig. 5b), with all of the pre-planned comparisons yielding non-reliable outcomes ($p > 0.20$; $f < 0.12$ for all comparisons). Cycle-average MTs ranged between 0.50 and 0.66 across all block for these groups. The similarity of MTs for the CF–FF and PF–KP groups suggests that CF–FF participants adhered to instructions and produced fast movements, with no online corrections (despite the provision of online feedback).

CF–FB participants were instructed to make whatever adjustments to the movement/cursor were necessary to

ensure that the target was acquired. The MTs exhibited by this group were markedly longer than those generated by the other participant groups in all cycles (Fig. 5b). Because we found the time at which peak velocity occurred was similar across all groups, the longer movement time for the CF–FB group were principally a result of an extended deceleration phase in which the online feedback was used to correct movement errors, i.e., the longer movement times are indicative of the implementation of feedback control. The use of this mode of control is likely to account for the increased MTs, with respect to the PREfinal cycle, exhibited by this group when they were initially exposed to the rotation (ROTinitial) ($p < 0.05$; $f = 1.05$). MT fell significantly within the training period (ROTinitial vs. ROTfinal: $p < 0.05$, $f = 0.79$), most likely reflecting reduced dependence upon feedback control as the feedforward commands became more specific to the rotated environment. Re-exposure to the non-rotated task (POSTinitial) resulted in movements that were significantly longer than those generated in the non-rotated cycle immediately prior to the rotation block i.e., PREfinal cycle ($p < 0.05$, $f = 0.79$). This increase in MT is consistent with a requirement to implement feedback corrections in order to compensate for the angular deviations (i.e., after-effects) generated in the feedforward segment of the movement.

Reaction time (RT)

Reaction time from presentation of each target to movement initiation in each trial is shown in Fig. 6. Exposure to the rotation led to increased RTs in the ROTinitial cycle for the PF–KP and CF–FF groups, with respect to RTs at completion of the PRE block (PREfinal vs. ROTinitial: $p < 0.05$; $f = 0.54, 0.92$ for the CF–FF and PF–KP groups,

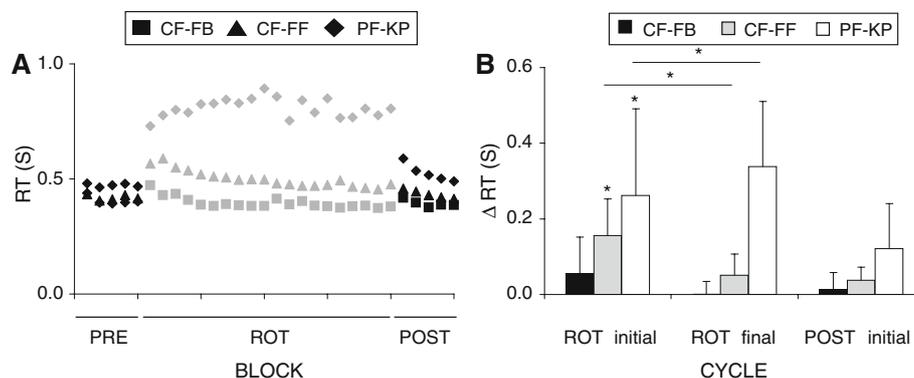


Fig. 6 Cycle-average reaction time. **a** Cycle-averaged RT in the PRE, ROT and POST blocks, averaged across the eight participants in each group (CF–FB squares; CF–FF triangles; PF–KP diamonds; also see key). **b** Mean ($\pm 95\%$ confidence intervals) difference (Δ) in RT in the ROTinitial, ROTfinal and POSTinitial cycles, relative to the

PREfinal cycle. A *asterisk* above the ROTinitial or POSTinitial bars indicates a significant change relative to the corresponding PREfinal value ($p < 0.05$). Significant changes between ROTinitial and ROTfinal are depicted by *horizontal lines and asterisk*

respectively; Fig. 6a, b). For the CF–FB group, this comparison did not reach statistical significance ($p = 0.13$; $f = 0.20$). For the CF groups, RT decreased within the ROT block, although this result did not quite reach statistical significance for the CF–FB group ($p = 0.07$; $f = 0.24$ for the CF–FB; $p < 0.05$, $f = 0.37$ for the CF–FF group). In contrast, RT *increased* for the PF–KP group within the ROT block ($p < 0.05$; $f = 0.27$). For the CF groups, RT in the POSTinitial cycle were not dissimilar to those prior to adaptation to the rotation (PREfinal) ($p = 0.67$, 0.60 ; $f = 0.06$, 0.13 for the CF–FB, CF–FF groups, respectively). For the PF–KP group, despite a substantial fall in RT when returning to the non-rotated task, POSTinitial RT was still somewhat elevated with respect to the PREfinal RT ($p < 0.05$; $f = 0.42$). RT did, however, continue to fall within the POST group to levels similar to that seen in the PRE block.

Discussion

When a motor command is generated in a novel environment the predicted sensory consequences of that motor command may not correspond with the actual sensory feedback received as a result of that command. Detection of this sensory error is critical to allow motor adaptation to occur. In the current visuomotor adaptation paradigm, the putative error signal was the discordance between task performance as indicated by visual feedback (indicating where participants moved to in relation to the intended target), and participants' proprioception based estimate of the location to which they moved. While proprioceptive information regarding the movement is clearly present *during* the execution of the task, we manipulated the timing of the visual feedback of task performance, such that it occurred during or following task execution. In this manner we were able to investigate whether temporal separation between feedback from the proprioceptive and visual systems (resulting in a delay between task execution and error detection) affected the extent and/or nature of feedforward adaptation to a novel visuomotor environment in this goal-directed two degree of freedom movement. This experiment represents a logical progression from previous work conducted in our laboratory (Hinder et al. 2008) that investigated a similar research question using an isometric paradigm. In the previously reported case there was, by definition, no movement of the limb. In neither study was there direct visual feedback of the task-relevant state of the limb (joint torque or position). Accordingly, the only difference between the isometric and dynamic tasks in regard to sensory feedback was the additional proprioceptive feedback resulting from movement of the limb that was available in the dynamic task.

Previous work in our laboratory (Shemmell et al. 2005) indicated that initial performance and the subsequent extent of adaptation in this two degree of freedom movement task varied as a function of target position, even in the absence of a visuomotor rotation. The magnitude of the inter-target differences reported by Shemmell and colleagues were, however, very small compared to those that are induced by the visuomotor rotation in the present study. Moreover, in the present study movements to “on-axis” (i.e., horizontal/vertical visual targets) and “off-axis” (i.e., diagonal visual targets) targets both required rotations of the forearm joints in *both* degrees of freedom (i.e., a combination of pronation/supination and flexion/extension) when exposed to the 60° rotation. For these reasons, a comparison of inter-target differences in performance and/or comparisons of targets requiring movements in one or two degrees of freedom is not conducted here. Instead we focus on results from target-averaged data.

By completion of the training (ROT) period, groups provided with continuous (concurrent) visual feedback of performance (CF–FF, CF–FB) or post-trial visual feedback of performance (PF–KP) had all attained a similar level of performance, compensating for the 60° CW rotation by about 50° (i.e., cursor paths following training still displayed about 10° of error; Fig. 6a, c). This under-compensation was also observed in our previous study in which an isometric task was examined (Hinder et al. 2008) and may be partially explained by anecdotal reports of some participants that they believed the rotation to be 45° (i.e., a rotation equivalent to one target position on the visual display). Residual angular errors of this magnitude are very similar, or indeed smaller, than those that persisted following the adaptation phase in a number of previous visuomotor rotation studies (e.g., Miall et al. 2004, Wang and Sainburg 2004, Krakauer et al. 2000, 2005, Hinder et al. 2007).

To determine if the action of making feedback corrections on the basis of the detected error signal promoted more rapid or more complete adaptation, or indeed changed the manner in which the adaptations occurred, we compared adaptation for participants provided with continuous visual feedback who were instructed not to make corrections to their movements, with that exhibited by participants provided with continuous visual feedback who were permitted to make corrections. We observed that the occurrence of corrections *was not* associated with feedforward adaptation that was any faster or more complete than that observed when only feedforward control was permitted. This finding replicates results recently reported by Tseng et al. (2007), indicating that detection of an error signal allows feedforward adaptation to a novel visuomotor environment but concurrent corrections on the basis of the detected sensory error do not necessarily facilitate this adaptation.

A fundamental feature of our experimental design was the use of contextual (colour) cues to enable the rotated and non-rotated task contexts to be identified. As such, participants were provided with the information required to issue the appropriate motor commands upon re-exposure to the non-rotated task, if indeed these commands were still available following learning in the rotated environment. Using this method, we were able to expand upon Tseng et al.'s work and investigate more closely the *nature* of the adaptation that occurred, with and without online visual feedback, and when online corrections were or were not permitted. Upon re-exposure to the non-rotated task (identified by the cue) significant aftereffects were observed for both CF groups, but *not* for PF–KP group. This finding is consistent with our previous work (Hinder et al. 2008) and confirms that that *timing* of the visual feedback of task performance (allowing a sensory error to be detected) has a profound effect on the nature of the feedforward adaptation that occurs in response to a novel visuomotor rotation. The results obtained when visual feedback of task performance was available during task execution are consistent with the established view that visuomotor adaptation occurs through an automatic modification of the visuomotor map that transforms sensory information into motor commands (Cunningham 1989; Krakauer et al. 1999). Furthermore, the nature of this adaptation was not affected by the absence or presence of online corrective actions on the basis of the online feedback.

We note that when first challenged with the rotation, reaction time (RT) increased to some extent for both CF groups (although this was only statistically reliable for the CF–FF group, Fig. 6). This increase in reaction time may be indicative of greater cognitive load (Klapp 1995) in the pre-movement (planning) period. With further exposure to the task, however, RT fell for CF groups to levels not dissimilar to those observed in the initial (pre-rotation) block, suggesting that execution of the task in the rotated context became more “automatic”. For these groups, performance improvements in the novel rotation were followed by significant aftereffects upon re-exposure to the non-rotated context. The fact that aftereffects occurred *despite* the provision of a salient cue that identified the change in task environment (consistent with the results of Miall et al. 2004) lends weight to the proposition that aftereffects were due to an automatic recalibration of the visuomotor map, and not due to misidentification of the task context. The re-adaptation that occurred in the post-training block is consistent with a re-modification of the visuomotor mapping to characterise the non-rotated task context.

In contrast, the results obtained from those participants who received post-trial visual feedback suggest that the

nature of their adaptation was quite distinct. Despite receiving feedback of the whole trajectory (i.e., the PF participants received the same amount of visual feedback) the fact that the information was provided following movement completion appears to have led to quite a different adaptation process. The data are consistent with the proposition that, when challenged with the rotation, these participants implemented an *explicit* (cognitive) strategy that enabled performance improvements to occur to the same extent as those subjects who were provided with continuous visual feedback. Consistent with this proposition, substantially longer reaction times were exhibited throughout the ROT block (Fig. 6). Over the course of the block, RT actually *increased* slightly, suggesting that the cognitive demand did not fall, and the level of automaticity achieved with CF did not occur with PF. In principle, an effective strategy would be to employ a visuomotor mapping appropriate for the original task environment, in conjunction with an offset of the visual coordinates of the target. Once the visual input (target location) had been shifted (or offset) by the required amount (direction and magnitude) the original visuomotor mapping could be used to transform this information into appropriate motor commands. A conceptual model of the putative modes of adaptation for the PF and CF groups is shown in Fig. 7. In this scheme, the (putative) cognitive component required by the PF group may account for the observed increase in RT.

For the post-trial feedback group re-exposure to the non-rotated context resulted in accurate performance (no aftereffects) and a substantial reduction in reaction time. This finding is also consistent with the proposed strategy-based model, insofar as a salient contextual cue (in this case the colour of the background screen) identifying the non-rotated task permitted these participants to immediately adopt an approach to the task that was indistinguishable from that which had been employed prior to the imposition of the rotation (i.e., they could simply abandon the cognitive component of the model shown schematically in Fig. 7b).

With a view to providing a quantitative means to assess the rate at which performance improvements occurred in the altered visual environments, we fitted power curves to the angular error data. In the first instance we chose to fit the curves to the cycle-average data, consistent with our analysis of the initial and final performance in each trial block in which we also employed cycle-average measures (also see Krakauer et al. 1999; Caithness et al. 2004). The *b* parameter provides a measure of the rate of performance improvement, and it did not differ between the three groups. This evidence suggests that the participants adapted to the imposed rotation at the same rate irrespective of the nature of the visual feedback (concurrent or post-trial)

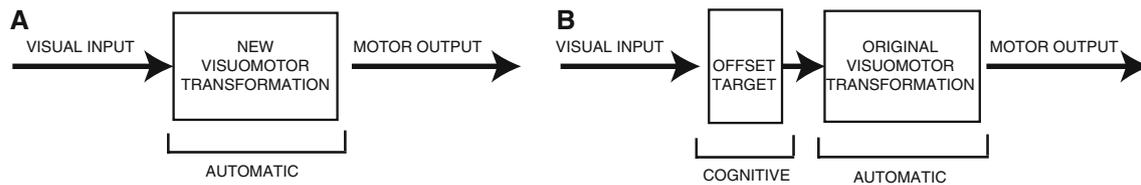


Fig. 7 Conceptual models for visuomotor adaptation. **a** Visual feedback of task performance during task execution permits adaptation through an automated modification of the visuomotor map that transforms visual inputs into motor outputs. **b** Post-trial visual

feedback results in adaptation that involves a cognitive process which offsets the presented target before utilising an unaltered visuomotor map

or task instruction (correct or do not correct movements online).

We also elected to investigate a potentially more sensitive means of examining the rates of adaptation since it was conceivable that cycle-averaging could mask subtle inter-group differences. We therefore also calculated *b* parameters on the basis of fits derived from the *individual* trials. Analyses based on these fits suggested that those participants who adapted using post-trial visual feedback did so more slowly than those participants who received online visual feedback. There was, however, no difference in the rate of performance improvement between the concurrent visual groups who were or were not permitted to make online corrections when moving towards visual targets. This particular result is consistent with a recent paper report by Franklin et al. (2008) who investigated adaptation to various force fields in the presence or absence of online visual feedback. They concluded that adaptation could occur in the absence of online visual feedback, but at a slower rate (determined by fitting curves to individual trial data for each participant) compared to when online visual feedback was available.

Our results suggest that despite cycle-averaging being a useful tool in allowing assessment of task performance across all target conditions rather than only considering the first/last trial of a particular epoch, care must be taken in interpreting the results, especially with respect to rates of adaptation derived from such data. Importantly, despite the potential caveat in interpreting the rates of adaptation in the present study due to the differing results obtained using the two methods, our interpretation of the results with respect to the expression of aftereffects remains robust. That is, we propose that adaptation to a novel visuomotor environment occurs principally by way of an automatic process when online visual feedback is available, but is mediated by the use of an explicit strategy when only post-trial feedback is provided.

As we alluded to in the [Introduction](#), the isometric task that we reported in a previous study (e.g. Hinder et al. 2008) by its very nature, denied participants *movement-related* proprioceptive feedback. Yet in isometric contractions there are other rich sources of sensory feedback.

Muscle spindle sensitivity is greatest at low muscle forces similar to those we studied (Burke et al. 1978), although saturation may occur at higher levels of force (Rymer and Dalmeida 1980). In addition, Golgi tendon organ activity increases monotonically over a wide range of muscle force (Houk et al. 1981). Importantly, however, in isometric contractions (quiescent) antagonist muscles generate little such proprioceptive feedback. This is in marked contrast to dynamic task utilised in the present report in which spindle afferent signals are typically generated in both the actively shortening muscle *and* the lengthening antagonist muscle. We were interested in determining if these differences in the nature of the proprioceptive information lead to a change in the way in which adaptation occurred under the different visual feedback conditions. We also refer the interested reader to the work of Bernier et al. (2007) who used tendon vibration as a means of *perturbing* proprioceptive feedback.

Despite the differences in the nature of the proprioceptive feedback that was available in the isometric and dynamic tasks, the patterns of adaptation to the imposed rotation were similar, i.e., the presence of movement-related proprioceptive information in the dynamic task failed to alter the finding that post-trial visual feedback is an insufficient basis to permit automatic adaptation to occur. Rather than the specific nature of the proprioceptive feedback affecting adaptation, we found that temporal separation between proprioceptive feedback associated with an action, and visual feedback of the result of that action (i.e., detection of the error), appears to prevent automaticity in visuomotor adaptation. Bernier et al. (2006) discuss the issue of temporal separation of proprioceptive and visual feedback with respect to ballistic reaching movements. They suggest that visual information during movement leads to a more accurate estimate of intersegmental dynamics of the moving limb i.e., one can determine the outcome of the immediately preceding motor command more accurately than in a delayed-visual feedback scenario. Indeed, our data suggest that an estimation of intersegmental dynamics thus derived promotes automatic adaptation of the visuomotor map, while post-trial feedback leads to adaptation via cognitive mechanisms,

whereby an automatic remapping does not necessarily occur.

McNay and Willingham (1998) considered the role of ‘recalibration of the perceptuomotor map’ and ‘strategies’ in visuomotor adaptation. Participants adapted to a 90° clockwise rotation of the (online) visual feedback during a line-tracing task. The extent of the adaptation attributable to the two proposed mechanisms was investigated in test trials in which participants were told that the rotation had been removed. Only performance improvements that occurred as a result of recalibrations might be expected to be apparent in that test, because an overt strategy could simply be abandoned if it was recognized as being inappropriate in the non-rotated context. McNay and Willingham’s results indicated that *throughout* training, a combination of recalibration and strategic approaches were used, indicating that the performance in the novel context never became fully automated. This finding is in contrast to the results for our CF groups: while these participants did not exhibit full adaptation to the rotation, their aftereffects were of comparable magnitude to the performance improvements observed during training suggesting that the adaptation was fully automatic. Moreover, our results suggest that for the group who received only PF in our study, adaptation may have been mediated principally by the use of a strategy. If any proportion of the performance improvements exhibited by this PF group were mediated by an automatic recalibration, corresponding aftereffects would have been anticipated. However, no such aftereffects were observed. The contrast between the results of the present study, and those reported by McNay and Willingham (1998) suggest that the balance between automatic adaptation and strategic intervention is labile and task specific. As such, further work aimed at promoting an understanding of the factors that influence this interplay would be beneficial.

In summary, we have shown that in this visuomotor adaptation task, involving a novel two degree of freedom dynamic adaptation task, detection of sensory error drives feedforward adaptation, and that online corrections (feedback mediated modifications) on the basis of the detected error do not necessarily improve the rate or the extent of the adaptation. These findings replicate and extend those of Tseng et al. (2007), showing that their finding can be generalised to other dynamic visuomotor adaptation paradigms. Secondly, we have shown that for visuomotor adaptation to occur in an automatic manner (Cunningham 1989; Krakauer et al. 1999), detection of visual errors must occur concurrently with task execution. This finding expands on our previous work using an isometric task (Hinder et al. 2008), and suggests that regardless of the nature of the proprioceptive feedback that is available, it is

the concurrent nature of visual feedback that permits automatic visuomotor adaptation.

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