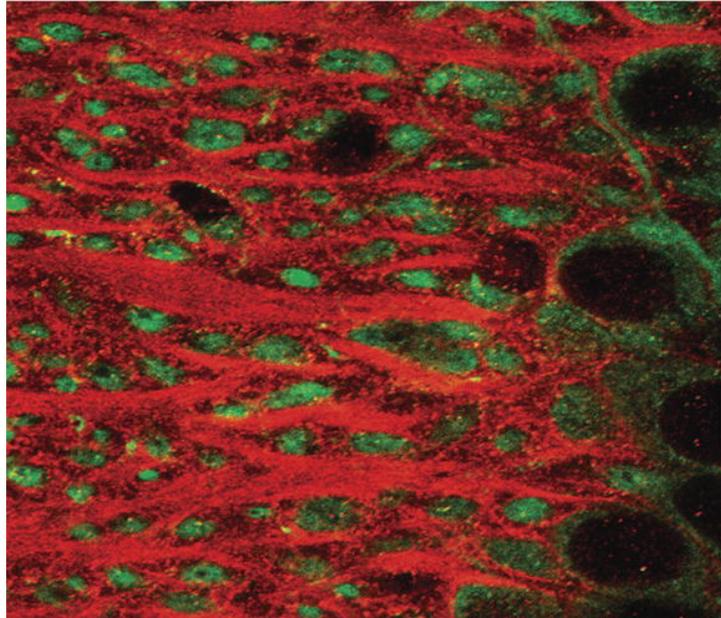


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RESEARCH

## Research Report

# The contribution of visual feedback to visuomotor adaptation: How much and when?

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## ABSTRACT

We investigated the role of visual feedback in adapting to novel visuomotor environments. Participants produced isometric elbow torques to move a cursor towards visual targets. Following trials with no rotation, participants adapted to a 60° rotation of the visual feedback before returning to the non-rotated condition. Participants received continuous visual feedback (CF) of cursor position during task execution or post-trial visual feedback (PF). With training, reductions of the angular deviations of the cursor path occurred to a similar extent and at a similar rate for CF and PF groups. However, upon re-exposure to the non-rotated environment *only* CF participants exhibited post-training aftereffects, manifested as increased angular deviation of the cursor path, with respect to the pre-rotation trials. These aftereffects occurred *despite* colour cues permitting identification of the change in environment. The results show that concurrent feedback permits automatic recalibration of the visuomotor mapping while post-trial feedback permits performance improvement via a cognitive strategy.

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## 1. Introduction

Unusual force fields and optical transformations such as those created by mirrors, prisms or computer-generated rotations create problems for an inexperienced person attempting a target-directed aiming task. For example, unusual forces can push the person off course and visual rotations typically cause people to move in the wrong direction. However, after attempting the task a few times a person typically learns to deal with the altered environment: their movement paths become straight with bell-shaped velocity profiles, almost identical to those originally produced in normal conditions. The person is said to *adapt* to the altered environment. Experiments have shown that adaptation typically involves changes in the feedforward motor commands

that take the alteration into account and compensate for it. Such changes in the commands can be interpreted as demonstrating that the process of adaptation involves creating or updating an internal model (e.g., Kawato, 1999). In the case of altered optical transformations, the model takes the form of a visuomotor map that transforms visual information into motor commands (Cunningham, 1989). Adaptation to a visual rotation then involves adjusting the visuomotor map so as to compensate for the magnitude and direction of rotation.

The adaptation process is driven by sensory feedback information about the discrepancy between the intended movement and the actual movement (the error). The visual and somatosensory systems are the most important sources of such information and normally both systems are likely to contribute to adaptation.

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However, it is known that vision alone can sometimes be sufficient for adaptation (Ghez et al., 1995) and somatosensory information can be sufficient for adaptation to novel force environments (Lackner and Dizio, 1994; Tong et al., 2002; Scheidt et al., 2005). In the case of altered visuomotor environments (e.g., those induced by prisms or rotations of feedback on a computer display), visual feedback concerning task performance is necessary for adaptation of aiming movements, when the success of the movement can only be determined visually. A recent study by Mazzoni and Krakauer (2006) indicated that in an out-and-back movement of a cursor, visual feedback in the first 100 ms of the movement, and a cursor depicting the reversal point of the movement, was sufficient to allow adaptation. This suggests that *continuous* visual feedback of the cursor position is not necessary for visuomotor adaptation, at least in dynamic visuomotor tasks (see also Krakauer et al., 1999; Miall et al., 2004).

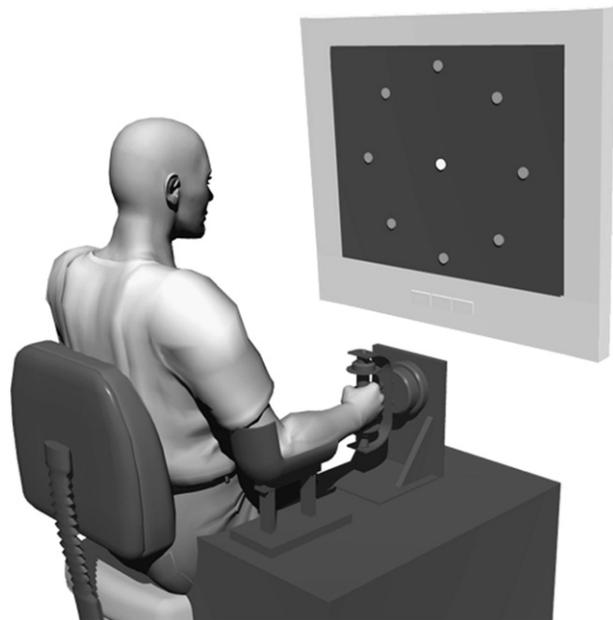
It is clear that visual feedback about various features of performance can be provided to a person in an aiming task. The most natural and obvious situation is one in which the person is able to see themselves move the working point as they attempt to acquire the target (complete concurrent feedback). Various restrictions can be introduced that allows a person to see only some of their performance (e.g., Mazzoni and Krakauer, 2006). An alternative is to deny a person visual feedback *during* performance but provide it after completion of the task. Depending upon the information actually provided, this type of feedback is called knowledge of results (KR) or knowledge of performance (KP). In KR only feedback about the outcome is provided: in an aiming task it might show the relative position of target and aiming device at completion. In KP, feedback about the movement is given: in an aiming task it might show the path taken to the target.

We sought to investigate how different types of visual feedback influence adaptation to a visual rotation. In particular, we asked whether the type of visual feedback (complete concurrent feedback or post-trial feedback) would affect how participants learned to compensate for the rotation. When aiming at a target in the presence of a visual rotation, it is possible to reach the target by moving in a direction that exactly cancels out the rotation. For example, if the rotation is 60° clockwise and the target is straight ahead, a movement directed 60° to the left will be in the direction of the target. Moving in the appropriate direction could be the result of a change in the visuomotor map. Alternatively, the person might learn the cognitive strategy of always aiming in a direction 60° to the left of the target. The method of interspersing occasional catch trials (Shadmehr and Mussa-Ivaldi, 1994), in which no rotation (perturbation) is applied, amongst a sequence of rotation trials is unable to distinguish between these two possibilities because in either case it would result in identical behaviour. For this reason we adopted a different approach. If participants were informed as to whether or not there was a visual rotation, for example with a colour cue, then the cognitive strategy of always aiming in a direction 60° to the left of the target, could be adopted when appropriate. In this case, we would expect little or no errors when participants return to a non-rotated environment. If, however, learning a 60° rotation results in a change in the visuomotor map, a return to a non-rotated environment would result in aiming errors in

the opposite direction of the rotation. We employed an isometric aiming task in which torques are applied to a fixed manipulandum and converted into movements of a cursor on a computer screen (Shemmell et al., 2005). This task removes potential complications due to the muscular and skeletal degrees of freedom available to participants in unconstrained reaching tasks, and eliminates the effects of anisotropic viscous and inertial properties of the limb (Pellegrini and Flanders, 1996).

## 2. Results

Participants produced isometric torques to move a cursor towards visual targets, presented on a computer screen (Fig. 1). Two groups of participants received continuous visual feedback of the cursor position (i.e., concurrent feedback, CF). One of these groups produced feedback modifications to correct errors (CF-FB), while one group only made feedforward responses (CF-FF). Two groups were provided with post-trial (PF) knowledge (feedback) of task performance (PF-KP) or task result (PF-KR) following task execution. Each group was exposed to a pre-training block (no rotation, PRE), a training period in which a 60° counter-clockwise rotation was applied (ROT), followed by a post-training



**Fig. 1 – Experimental set-up.** Participants held the manipulandum and controlled cursor movement via isometric flexion–extension (up–down cursor movement) and pronation–supination (left–right cursor movement) torques of the elbow–forearm complex. Torques were measured by the force/torque transducer positioned behind the handle. When participants relaxed their arm in the restraint, zero torque was registered, 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.

block (no rotation, POST). The screen colour in each block allowed the nature of the task environment (rotated/non-rotated) to be identified (see *Experimental procedure* for more information).

Fig. 2 shows examples of the cursor paths for a single participant in each of the four groups. Paths are shown for the first

and last trial to the flexion and extension target in each block. Differences between the latter stages of the cursor paths produced by the CF-FB group (Fig. 2B) and those generated by the three other groups reflect the fact that CF-FB participants were instructed to make corrective responses when required, while

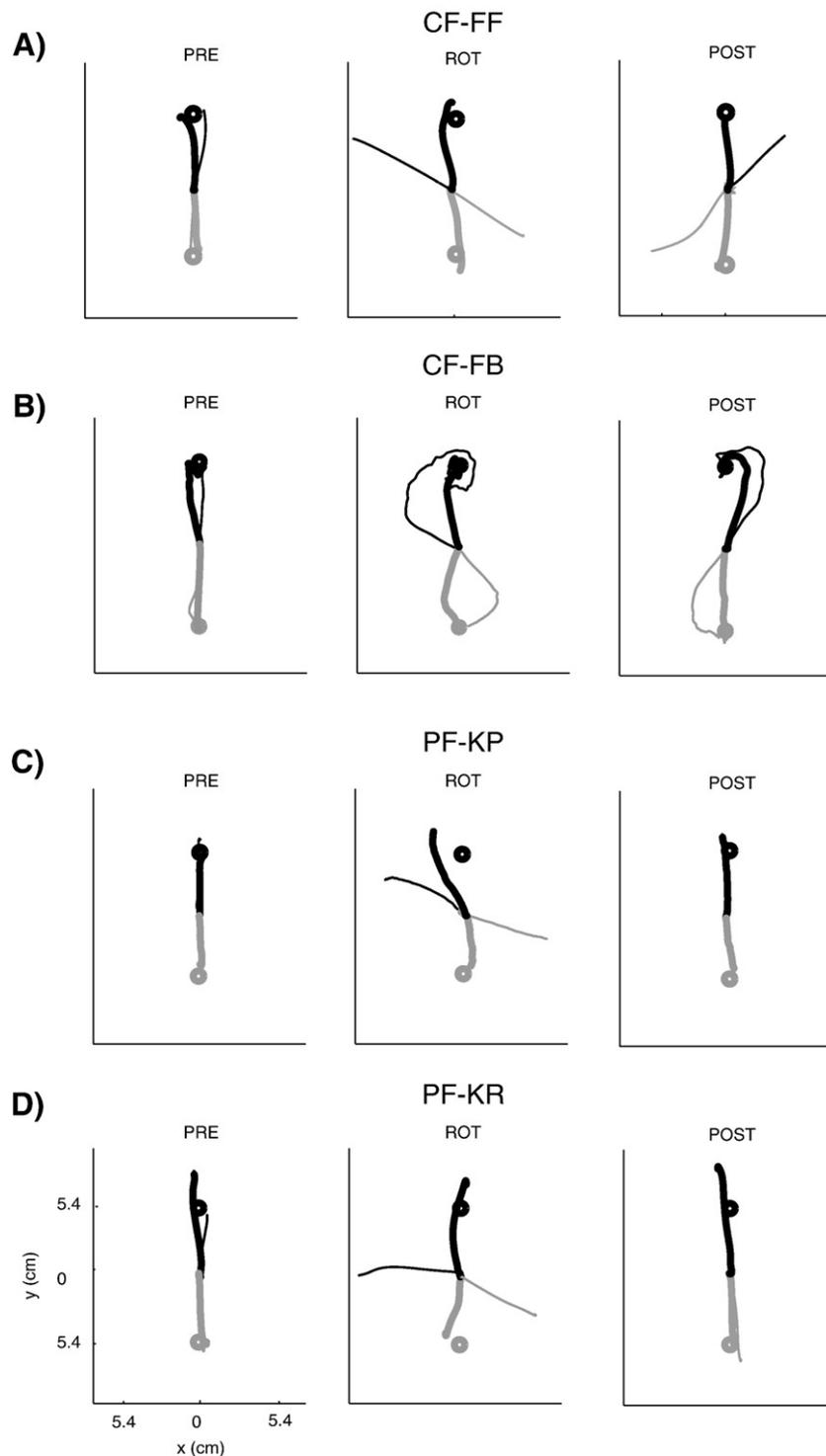


Fig. 2 – Cursor paths in the first and last trials of the PRE, ROT and POST blocks, for flexion and extension targets. Paths are shown for the first (thin line) and final (thick line) trial in each trial block (PRE, left; ROT, centre; POST, right) to the flexion (black targets and paths) and extension (grey targets and paths) targets. A) CF-FF B) CF-FB C) PF-KP and D) PF-KR groups.

the other three groups relied solely on feedforward commands. The initial segments of the cursor paths, prior to the time at which any online corrective responses could have been implemented, may however be used to characterise and compare the feedforward performance across all groups. From the kinematic data depicted in Fig. 2 we obtained cycle-averaged angular errors (measured at peak rate of isometric torque, see *Experimental procedure*) in the PRE, ROT and POST block for each participant in each group. Fig. 3A shows the participant-averaged angular error values for all cycles within each of the trial blocks.

Fig. 2 indicates (qualitatively) that in the PRE block, all participants produced torques that resulted in fairly accurate movement of the cursor towards the target (Fig. 2, left hand column; Fig. 3A, PRE block cycles). There is no obvious change in cursor path or angular error between the early and late trials within the PRE block suggesting this torque-cursor movement mapping was intuitive. Exposure to the 60° CCW rotation resulted in displacement of paths in the direction of the rotation for all groups (Fig. 2 central column, thin traces; Fig. 3A initial ROT block cycles). The fact the errors were somewhat less than the imposed rotation (i.e., 60°) indicates that a certain degree of learning occurred within the first cycle of trials. With learning, all groups modified feedforward motor commands such that cursor paths were more accurately directed towards the target (Fig. 2 central column, thick traces; Fig. 3A ROT block final cycles) with less need for feedback corrections for the CF-FB group (smaller “hooks” on the cursor paths).

For the both the CF-FF and CF-FB groups, re-exposure to the non-rotated environment (POST block) resulted in paths that initially deviated from the start-target line in the opposite direction to the deviations exhibited in the first exposure to the rotation (Fig. 2C–D, final column, thin traces; Fig. 3A POST block cycles, solid lines), i.e., substantial aftereffects were apparent. For the CF-FB group, online corrections allowed target acquisition to be achieved. By the end of the POST block, paths had been become significantly straighter for both CF groups. In contrast, the PF groups produced paths from the onset of the POST block that were accurately directed towards targets (Fig. 2A–B right hand column, thin traces; Fig. 3A, POST block cycles, dotted lines), i.e., *no aftereffects were apparent*. 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*.

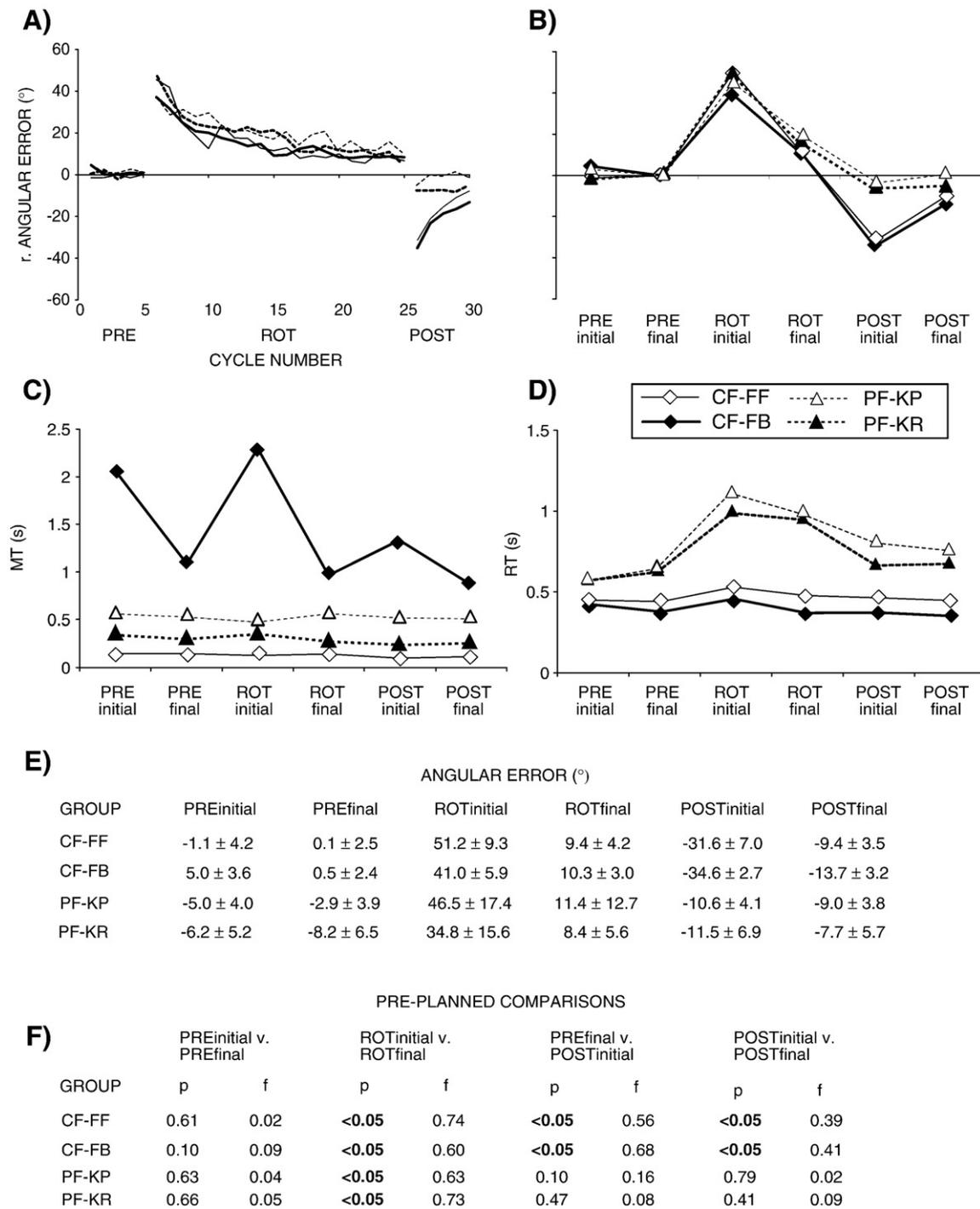
Power-curves were fitted for cycle-averaged movement time, reaction time and angular error data for each participant and fitted values for the initial and final cycle in each trial block were calculated (see *Experimental procedure*). Statistical analyses using these fitted values and actual data values for the corresponding cycle realised similar outcomes (with regard to statistical significance), with comparable effect sizes, in the pre-planned comparisons, indicating that the two methods are comparable. In this paper, we report the power-fit data for the reasons outlined in the *Experimental procedure*. The co-efficient of variability associated with each fit ranged from 0.25–0.98. Fig. 3B–D shows the means of the fitted values for each dependent variable, averaged over the 8 participants in each group. Fig. 3E–F show the mean ( $\pm 95\%$  confidence intervals) fitted values for angular error and pre-planned comparisons, respectively.

### 2.1. Angular error — a measure of the feedforward performance

We investigated *feedforward* performance improvements in the task by considering angular deviations of the cursor paths in the early part of the task. The CF-FF group received continuous visual feedback of task performance, but were instructed not to make corrective movements. To corroborate that these participants adhered to task instructions and did not make modifications of the cursor trajectory in the latter part of each trial, we compared “early” angular error (at peak rate of torque development) to that angular error recorded at the end of the trial (“late” angular error). Late angular error was calculated using the same cycle-average fitting procedure that we used for the all dependent variables (see *Data reduction and analysis*). Two-way ANOVA (early/late  $\times$  6 fitted positions, i.e., PREinitial, PREfinal, etc) failed to reveal any significant differences between the early and late angular error for the CF-FF group (early/late main effect:  $p=0.93$ ,  $f=0.09$ ).

Furthermore, we confirmed that the straightness of the cursor trajectories produced by the CF-FF was not dissimilar to the straightness of those of the PF groups. A comparison of the differences between early and late angular error in each of the 6 fitted positions across the three groups was not significant (Two-way ANOVA, group main effect  $p=0.16$ ;  $f=0.15$ ). The magnitudes of these differences did not exceed 3.5° in the 6 fitted cycle positions across the three groups, and averaged 1.8°. The small magnitude of the differences suggests that participants did not significantly alter the direction of the cursor between the point at which we assessed feedforward adaptation (location of peak rate of torque development) and completion of each trial, i.e., cursor paths were not substantially bowed in either direction. These results allow us to draw conclusions on the basis that the CF-FF did indeed make uncorrected ballistic force impulses. Furthermore, we can conclude that participants in these groups were able to produce the torques in the two task degrees of freedom simultaneously — substantial differences in the timing of the peak torques in the orthogonal torque directions would have lead to larger changes in angular error between the early and late periods of the trial.

Initial analysis revealed that angular error values ( $\theta$ ) calculated at 100 ms and at the peak rate of torque development were very similar. Indeed, RM ANOVA indicated that the fitted values of angular error at 100 ms and peak rate of torque development were not dissimilar for any group ( $p>0.18$ ). Thus, it appears that despite peak rate of torque development occurring after 100 ms for all groups (generally 100–200 ms) those groups provided with visual feedback did not make feedback modifications to alter the cursor trajectory. Thus, the measure of angular error at peak rate of torque development can accurately represent feedforward performance. Furthermore, the pre-planned comparisons (see *Data reduction and analysis*) yielded equivalent results with similar effect sizes for both measures of angular error. Here we report the results for angular errors measured at peak rate of torque development. Using this measure, we avoid the possibility that the intergroup differences in movement times (i.e., that 100 ms following movement onset represents a different position within the movement with respect to peak rate of change of torque) may affect the integrity of the results.



**Fig. 3 – Angular errors, movement times and reaction times. A)** Cycle-averaged angular errors in the PRE, ROT and POST blocks, averaged across the eight participants in each groups (CF-FF: thin solid line; CF-FB: thick solid line; PF-KP: thick dotted line; PF-KR: thin dotted line). **B)–D)** Mean fitted values for angular error, reaction time and movement time, in the initial and final cycle of each of the three trial blocks. (Note that angular error data in panels A and B are shown relative to the final cycle of the PRE block, i.e. any small offsets relative to a straight-line cursor path have been removed to allow better inter-group visual comparisons). The key below panel B enables identification distinguishes between participant groups. **E).** Mean ( $\pm 95\%$  confidence intervals) fitted values for angular error. **F).** *p*-value and effect size (*f*) for each of the angular error pre-planned comparisons. Bold font denotes significant comparisons at the a-priori level ( $\alpha=0.05$ ).

Angular errors in the PRE block were of low magnitude (Fig. 2A–B, E), and there was no significant changes in  $\theta$  over the course of the PRE block for any participant group ( $p=0.10$ – $0.66$ ;

$f=0.02$ – $0.09$  for all groups). The low magnitude of  $\theta$  throughout the PRE block, together with the small effect size of the PREinitial–PREfinal comparisons, suggests participants found

the angular control of the torque quite intuitive. As expected, initial exposures to the rotation led to increased  $\theta$  relative to the PRE trials. By completion of the training (ROTfinal), participants from all groups learned to compensate for the imposed rotation, significantly reducing the  $\theta$  relative to that error exhibited in the ROTinitial cycle ( $p < 0.05$  for all groups;  $f = 0.60$ – $0.74$ , Fig. 2A–B, E). To assess potential aftereffects as a result of performance improvements within the rotated environment, we compared  $\theta$  in the cycle immediately prior to (PREfinal) and following (POSTinitial) the rotation block. For both CF groups, the comparison indicated significant differences and large effect sizes ( $p < 0.05$ ;  $f = 0.56$ – $0.68$ ). In contrast, for the PF groups the comparison was not significant ( $p = 0.10$ – $0.47$ ;  $f = 0.08$ – $0.16$ ) and was associated with small effect sizes. For the CF groups, relearning occurred within the POST block, with the POST-final cycle exhibited angular errors of lower magnitude than the POSTinitial cycle ( $p < 0.05$ ,  $f = 0.39$ – $0.41$ ). For the PF groups, there was no significant change in  $\theta$  within the POST block ( $p = 0.49$ – $0.79$ ,  $f = 0.02$ – $0.09$ ), presumably because initial performance was not dissimilar to that at completion of the PRE block, and thus relearning was not required.

## 2.2. Inter-group comparisons of angular errors and learning rates

The initial effect of imposing the rotation, i.e., the magnitude of the change in  $\theta$  between the PREfinal and ROTinitial cycles, was not dissimilar across groups ( $43.1^\circ$ ,  $49.4^\circ$ ,  $51.2^\circ$  and  $40.5^\circ$  for the PF-KR, PF-KP, CF-FF and CF-FB groups, respectively: One-way ANOVA  $p = 0.68$ ,  $f = 0.22$ ). The fact that these values are somewhat smaller than the imposed rotational of  $60^\circ$  change can be explained by the not insignificant reductions in angular error that occurred over the course of the (16) trials of the first cycle for each group. Indeed, angular errors on the very first ROT trial were around  $60^\circ$ . Performance in the final cycle of the ROT phase ( $8.4^\circ$ ,  $11.4^\circ$ ,  $9.4^\circ$  and  $10.3^\circ$  PF-KR, PF-KP, CF-FF and CF-FB groups, respectively) was not distinguishably different across the four participant groups (One-way ANOVA  $p = 0.95$ ,  $f = 0.11$ ), nor did the degree of adaptation (reduction in  $\theta$ ) between the first and the last cycle of the ROT block ( $26.4$ ,  $35.0^\circ$ ,  $41.8^\circ$  and  $30.8^\circ$  for the PF-KR, PF-KP, CF-FF and CF-FB groups, respectively) vary between groups (one-way ANOVA,  $p = 0.24$ ,  $f = 0.36$ ). These results provide compelling evidence that the absence of aftereffects in both PF groups is not a result of these groups compensating for the rotation to a lesser degree than the CF groups.

Furthermore, to exclude the possibility that PF groups adapted more slowly than the CF groups, and were thus at a different stage of the learning process when re-exposed to the non-rotated environment, we compared the rates at which the different groups reduced angular error with training. One-way ANOVA of the “b” parameter (decay constant) from the angular error power-fits provided no evidence of a difference between conditions ( $b = -0.53$ ,  $-0.39$ ,  $-0.66$ ,  $-0.49$  for the PF-KR, PF-KP, CF-FF and CF-FB groups, respectively; One-way ANOVA  $p = 0.22$ ;  $f = 0.32$ ). Taken together, these inter-group comparisons offer no support for the supposition that participants adapted less, or more slowly in the PF groups compared to the CF groups.

To eliminate the possibility that cycle-averaging masked aftereffects that were present in the PF groups but which were

quickly (within a few trials) eliminated (re-learning in the non-rotated environment) we conducted an analysis of individual trials. For both the PF groups, the gradient of the linear regression was not significantly different to zero ( $p > 0.34$  in both cases), indicating there was no significant trend in angular error within the 16 trials of the first cycle of the POST block. In contrast for both CF groups the gradient of a linear regression of the first 16 trials (first cycle) of the POST block was significantly less than zero ( $p < 0.05$ ), indicating significant incremental error reductions (reduction of aftereffects). Thus, the lack of aftereffect noted for the PF groups using cycle-average data was not because the aftereffect was quickly reduced such that the average aftereffect over the first 16 trials (i.e., the first cycle) was imperceptible. For the CF groups, despite the reduction of the angular error within the first cycle for CF groups, the aftereffects were still significant when analysing cycle-averaged data.

## 2.3. Movement time — a measure of overall task performance

MTs varied little between and within blocks for the CF-FF and PF groups (Fig. 3C), with all of the pre-planned comparisons yielding non-significant results. MTs ranged between  $0.24$ – $0.55$  across these groups. MTs for the CF-FF group were comparable to those for the PF groups indicating that the CF-FF participants adhered to instructions and produced a ballistic torque impulse with no online corrections. The only group who were instructed to make corrective adjustments within the trial such that the target was acquired was the CF-FB group. Substantially longer MTs in all cycles compared to the other participant groups reflect the implementation of feedback control to acquire the target. For the CF-FB group, MT decreased over the course of the PRE block ( $p < 0.05$ ,  $f = 0.69$ ). The large corrections required upon re-exposure to the rotation lead to an increase in MT. However, MT was subsequently reduced within the course of the ROT block ( $p < 0.05$ ,  $f = 0.99$ ). Upon initial re-exposure to the non-rotated task (POSTinitial), MT was not significantly different to that in the non-rotated cycle immediately prior to the rotation block (i.e., PREfinal,  $p = 0.12$ ,  $f = 0.16$ ). Within the course of the POST block, MT fell ( $p < 0.05$ ,  $f = 0.31$ ) to  $0.64 \pm 0.06$  s. The reductions of movement time within each block are likely to reflect reduced dependence upon online, feedback corrections, as the feedforward model became more accurate.

## 2.4. Reaction time (RT)

RTs in the first and last cycle of the PRE block were not significantly different for the CF-FF and PF groups ( $p = 0.43$ – $0.76$ ;  $f = 0.06$ – $0.15$ ). For the CF-FB group, there was a trend for a reduction in RT, although this was not significant ( $p = 0.10$ ,  $f = 0.34$ ). Exposure to the rotation lead to increased RTs for all participant groups, although the relative increase was 3 times larger for the PF groups compared to the CF groups (Fig. 3D). For both the PF groups, RT remained at this elevated level throughout the rotation block, i.e., there was no significant difference in RT in the initial and final cycle of the ROT block ( $p = 0.55$ – $0.71$ ;  $f = 0.05$ – $0.12$ ). In contrast, for the CF-FF ( $p = 0.05$ ,  $f = 0.39$ ) and CF-FB ( $p < 0.05$ ,  $f = 0.72$ ) groups shorter RTs were recorded in the ROT-final cycle, compared to the ROTinitial cycle, with RT falling to levels comparable to the PRE block for these groups. For all

participant groups upon initial re-exposure to the non-rotated task (POSTinitial) RTs were not dissimilar to RTs in the final cycle prior to rotation learning, i.e., the PREfinal cycle ( $p=0.26$ – $0.44$ ;  $f=0.12$ – $0.24$ ). Finally, no significant change in RT occurred within the POST block for any of the participant groups ( $p=0.37$ – $0.90$ ;  $f=0.02$ – $0.17$ ).

### 3. Discussion

We investigated the effects of the type of visual feedback (concurrent or post-trial feedback) and of task instruction (“modify path” versus “do not modify path”) on participants’ ability to adapt to a novel visuomotor rotation in an isometric target acquisition task. All groups of participants were able to compensate for the visual rotation to a similar degree over the course of training. The compensation had a major feedforward component as the angular error in the initial direction of movement reduced significantly with training in all groups. However, the performance of the groups differed in the post-training (POST) block in which participants were transferred back to an environment without rotation.

The groups who received continuous, concurrent visual feedback during task execution (CF groups) showed classic aftereffects in the POST block in which their cursor paths were displaced in a direction opposite to that observed when first exposed to the rotation. Making feedback modifications to correct the observable performance errors *did not* affect feedforward adaptation to the novel rotation, compared to those participants instructed not to make modifications to the cursor path. In contrast, the groups who received only post-trial visual feedback (PF) of performance did not display any discernible aftereffects—performance in the POST block for these groups was not statistically distinguishable from performance prior to training. These results demonstrate that the contextual colour cue indicating that the environment was no longer rotated permitted the PF groups to shift back to a performance strategy suited to the non-rotated environment but did not permit the CF participants to do so.

In this isometric task proprioceptive feedback arising from limb motion was diminished compared to dynamic reaching tasks. We hypothesised that any manipulations of visual feedback of task performance in the isometric task may have a more profound effect on the manner in which the adaptation to the altered environment occurred compared to manipulations of visual feedback in a dynamic reaching task. The precise nature of the visual feedback was found to have a significant effect on the manner in which adaptation occurred. The difference between the CF and PF groups is consistent with them learning to compensate for the rotation in different ways. The pattern of performance shown by the CF groups indicates that the automatic visuomotor mapping that transforms visual information into motor commands had been adapted to compensate for the rotation. Alterations of the automatic process of transforming sensory information into motor commands is the usual explanation for the aftereffects observed in dynamic (Cunningham, 1989; Krakauer et al., 1999; Shadmehr and Mussa-Ivaldi, 1994) and isometric (Hinder et al., 2007) adaptation studies. This alteration to the visuomotor mapping could not simply be reversed on the basis of a contextual cue, but rather had to be unlearned iteratively over the course of the POST block.

The absence of aftereffects in the PF groups suggests that something different may have taken place during training in these groups. One possibility is that participants in these groups were able to create a new visuomotor map specific to the rotation and simultaneously retain the original mapping and retrieve it in the POST block. A more likely alternative is that no automatic adaptation of the visuomotor mapping took place in the PF groups; rather they were able to learn an explicit (cognitive) strategy of moving in a direction that compensated for the imposed rotation. This strategic approach could be considered as utilising the original visuomotor mapping with a learned “offset” of appropriate magnitude and applied to the visually-presented target, such that the appropriate motor commands were issued. Use of such a strategy would be expected to be associated with longer reaction times due to increased cognitive processing between stimulus presentation and onset of motor commands (Henry and Rogers, 1960; Klapp 1995). Consistent with this, we found that RTs for the PF groups were about 65% higher throughout the ROT block, compared to RT for the same groups in the PRE block (Fig. 3D). Upon re-exposure to the non-rotated environment, as indicated by the screen colour, RT fell to levels similar to those observed in the PRE block.

It is unlikely that the longer RTs for the PF groups were simply due to processing of the post-trial visual feedback presented in the preceding trial. As indicated in the *Experimental procedure*, 3–4 s were available to process the visual information prior to presentation of the next target. It seems unlikely that it would take this long to process the visual information. Indeed, we saw no systematic variation in RT as a function of the random-length fore-period. Moreover, the large increases in RT for the PF groups in the ROT block were not seen for the CF-ff group who also had to process visual information following each trial within a similar time period.

Upon initial exposure to the rotated environment, RT also increased somewhat (20%) for the CF groups. Some of these CF participants, as well as the PF participants, reported trying to aim not at the presented target, but at an imaginary target. This suggests that in both visual feedback conditions (CF and PF) participants were aware of the nature of the visual distortion and that in the initial stages of learning, CF participants may have also adapted to the new environment using an explicit strategy. However, for the CF groups, this strategy quickly became automated, requiring fewer cognitive resources, indicated by RTs that quickly fell to levels comparable to the respective PRE block (Henry and Rogers, 1960; Klapp 1995). As mentioned previously, for the PF groups the task in the rotated environment remained much more cognitively demanding and never attained the level of automaticity as it did for those in the CF groups.

The relationship between implicit (automatic) and explicit (cognitive) processes has been extensively studied within sequence learning paradigms (e.g., choice reaction time experiments). However, much less is known about the contribution these processes to motor learning. In this context, implicit adaptation may be considered as automatic adaptation (for example modification of an internal model of the task environment or recalibration of a visuomotor map) while an explicit strategy may involve cognitive strategies to achieve accurate performance in the same novel task. Mazzoni and Krakauer (2006) recently addressed this issue in a novel paradigm which

introduced a conflict between implicit and explicit processes by instructing participants to counter a visuomotor rotation using a cognitive strategy in a pointing task (Mazzoni and Krakauer, 2006). Participants were instructed that to achieve accurate movements towards the specified (goal) target they should actually aim at the *neighbouring* target. Rather than exclusively relying on this explicit strategy, implicit adaptation occurred *simultaneously*. There was an unconscious amendment of the internal mapping that transforms sensory information into motor commands, such that the incongruity between the planned and actual trajectory to the neighbouring target was reduced. This had the consequential effect of increasing errors (degrading task performance) relative to the specified (goal) target. The authors suggested that congruity between planned and executed trajectories (i.e., *implicit adaptation*), and not terminal error relative to the goal target, drives adaptation to novel visual environments, suggesting that the motor system preferentially compensates *implicitly* to novel visuomotor environments.

Our task did not introduce a conflict by instructing participants to employ an explicit strategy, as in Mazzoni and Krakauer's study (2006). Rather, we manipulated the visual feedback in an attempt to determine if this affected the mechanisms employed by the motor system to compensate for the imposed rotation. We propose that the remapping of the visuomotor transformation that occurred for the CF groups in our study, is automatic or implicit adaptation driven by concurrent feedback of task performance and kinaesthetic feedback of task execution. When concurrent feedback information is not available explicit strategies may be used as an alternative to the implicit approach, without degradation in the extent or rate of adaptation. The proposition that the motor system adapts automatically through modification of the feedforward internal model or visuomotor relationship, but that *concurrent* sensory feedback of task execution and performance error is required to drive this adaptation, is worthy of further investigation.

## 4. Experimental procedure

### 4.1. Participants

Thirty-two self-reported right-handed participants (18 male, 14 female, 19–44 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.

### 4.2. Apparatus

Participants sat in a height-adjustable chair 65 cm from a computer screen, positioned at eye level. The right arm was placed in a padded brace with the elbow flexed at 90° and the forearm in a neutral position. Participants grasped an instrumented vertical cylindrical handle, with pads positioned above and below in order to minimise movement of the hand (Fig. 1, also see Shemmell et al., 2005 for further details). Force and torque were recorded at 2000 Hz and stored on a personal computer.

### 4.3. Procedure

A yellow dot at the centre of the 10.8 cm square visual feedback screen, representing the start zone (zero torque), was presented at the beginning of each trial. A white cursor indicating the current level of applied isometric torque was visible in the pre-movement period when the applied torque was less than 10% of the target torque. This cursor appeared in the centre of the screen (coincident with the start zone) when participants relaxed their arm in the elbow brace. The visual feedback around the centre of the screen allowed participants to make small adjustments to cursor position prior to each trial, but precluded them from investigating the torque-cursor movement relationship over the wider workspace.

Each trial began with a random period of 1–2 s, during which participants were instructed to keep the cursor within the start zone. One of eight targets, equally spaced at 45° intervals around, and at a constant distance of 5.4 cm (i.e., half way to the edge of the visual workspace) from the start zone, was presented, accompanied by an auditory tone. In this manner, subjects were exposed to the full *radial* workspace. Participants were instructed to react quickly upon presentation of the target, and move the cursor towards the target as quickly as possible by producing isometric torque in one or both of the two degrees of freedom of the elbow-forearm complex (flexion-extension; pronation-supination). The magnitude of the cursor displacement was directly proportional to the level of isometric torque generation.

### 4.4. Experimental groups

Four groups of eight participants undertook the experiment with varying types of visual feedback (Table 1). Two groups of participants were presented with continuous visual feedback of the cursor position over the whole workspace during the trial (i.e., concurrent feedback, CF), while two groups were provided with post-trial feedback (PF) following task execution.

Both PF groups, and one CF group were instructed to react quickly to the presentation of each target and generate one, fast, un-corrected torque to move the cursor towards the target. Participants subsequently relaxed their arms which returned the cursor to the start zone for the next trial. Thus, for these three groups, we assessed performance in the absence of feedback modifications.

One PF group was presented with knowledge of results (KR; PF-KR group) depicting the final cursor position achieved during the trial. The target to which they had aimed was visible as a red dot while a green dot depicted the final cursor position. Final position was defined as the screen position corresponding to the flexion-extension (y-component) and pronation-supination (x-component) torque components of the maximum (i.e., asymptotic) resultant torque. The other KR group was provided with a green trace depicting the cursor path, from movement onset (see Analysis section) to final position (movement offset, i.e., maximum torque) along with the red target dot i.e., knowledge of performance, KP (PF-KP group). Following production of the isometric torque impulse, PF participants relaxed and waited for the feedback of their result/performance, which was presented 4 s after the trial began. After a 2 s feedback period, the next trial began automatically. Therefore, there was a 6 s interval between the onsets of the fore-periods in consecutive trials. Participants

**Table 1 – Task instructions and visual feedback conditions for the four participant groups**

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

in the CF group instructed *not* to make any online (feedback) corrections to the cursor position were provided with online visual feedback throughout the task but *could not* this feedback to make modifications. Accordingly, this group will be referred to as the visual feedforward control group (CF-FF). The fore-period of consecutive trials began at 6 s intervals, as per PF groups.

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 that the cursor representing the magnitude and direction of applied torque in each trial coincided with the target zone for at least 100 ms). This task required visual feedback to be used to facilitate online (feedback) 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 executed.

For the CF-FB group, when the cursor was held within the target zone, defined as a region  $\pm 5\%$  around the specific target torque requirements, for 100 ms a second auditory tone sounded, at which point participants relaxed and the cursor returned to the start zone. During trials in which participants failed to acquire the target (“unsuccessful trials”), there was no second tone and the target disappeared 9 s after the fore-period began. Such trials (<2% of total trials) were not repeated, and the next trial

began as normal. For this group, movement offset was defined as the point 100 ms before the second tone. To give CF-FB participants sufficient time to make online corrections to acquire the target, a longer trial length 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 slower than the other three groups, the longer movement times for the CF-FB group ensured comparable time periods between completion of the task in one trial and commencement of the subsequent trial across all groups.

#### 4.5. Experimental paradigm

All groups undertook a short practice block of trials (3 trials per target), in which online feedback of the cursor position was available. No rotation of the cursor was applied. The purpose of this block was twofold. Firstly it ensured that participants understood how to produce torque to control the cursor in each orthogonal direction. Secondly, it enabled that participants appreciated the levels of torque required to move to the vicinity of the target. This would ensure that in subsequent blocks for the PF groups the position of the cursor relating to maximum torque production was not beyond the limits of the visual display. Despite provision of online feedback in this short pre-experimental block, PF-KR, PF-KP and CF-FF participants were instructed to make one rapid, un-corrected cursor movement towards the target- as was the instruction in the subsequent experimental blocks. These trials also taught the CF-FF group to resist any urge they had to produce corrective torques on the bases of the visual information that was available to them. These trials were not included in any statistical analysis. CF-FB participants made modifications of their torque, as required, to acquire the presented target.

All groups subsequently undertook three experimental blocks of trials. All trials in a block were conducted with a specific relationship between the direction of torque production and direction of the ensuing cursor movement. The background colour of the display — during both the trial and in the post-trial feedback period — indicated the operative relationship between the direction of torque production and the resulting displacement of the cursor. The PRE block (10 trials to each target; 80 trials total) was undertaken with veridical cursor feedback. Elbow flexion and extension torques resulted in vertically upward, and downward, cursor movement, respectively. Pronation and supination torques resulted in cursor movement to the left, and right, respectively. Within each 16-trial cycle, two trials to each target were undertaken; the order of target presentation within the cycle was randomised. The PRE block thus consisted of 5 such cycles. All PRE trials were conducted with a dark grey background. Participants could therefore associate the intuitive (or veridical) torque production-cursor movement mapping 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 perturbed by way of a 60° counter-clockwise (CCW) rotation, with respect to the direction of torque production (ROT block). This block consisted of 40 trials to each target (20 cycles, 320 trials total). All ROT trials were performed with a blue background that was

maintained during the trial and post-trial (for PF groups) feedback periods. Participants were thus provided with the facility to associate the novel torque production–cursor position mapping/relationship with the blue screen. Finally, participants were re-exposed to the veridical mapping which they had previously encountered in the PRE block (POST block). A dark-grey screen was used, as in the PRE block, allowing the restoration of the original torque–cursor 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 discussed above were applied in each three trial blocks for each group (i.e., the CF groups received online feedback in the PRE, ROT and POST blocks, while PF groups received only post-trial feedback in each block). In total, the experimental protocol lasted ~1 h. 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 torque production 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.

The torque magnitude required to attain each target was identical across all participant groups, experimental blocks and targets. Torque requirements were well within the capabilities of all participants (10–20% of participants' maximum torque capacity) to minimise fatigue. For targets representing combinations of torques in two degrees of freedom, the vertical (flexion/extension) and horizontal (pronation/supination) torque components were determined as the cosine of the subtended angle between the target direction and the single degree of freedom target, multiplied by the single degree of freedom torque. In the ROT block, the vertical and horizontal torque components were re-calculated according to the imposed 60° CCW rotation (see also Hinder et al., 2007).

#### 4.6. Data reduction and analysis

Torque 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.

Movement time, MT, from movement onset to target acquisition (CF-FB group) or movement onset to maximum resultant torque production (all 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 would be predicated upon initial exposure to the rotation due to increased requirements for feedback modifications to acquire the target. Reduced MT within each block (PRE, ROT, POST) would be expected for two

reasons: firstly, more accurate feedforward commands would result in only small feedback corrections being required, and secondly with learning, participants should learn to implement the required feedback corrections more quickly. Angular error,  $\theta$ , was calculated at two positions within the trial: 100 ms after movement onset, and at the peak rate of (resultant) torque development. 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 rate of torque development, 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 rate of torque development was calculated to take account of differences in movement times between participant groups (see results) i.e., 100ms following movement onset represented a different position in the trial, with regard to acceleration and deceleration phases. Hand path characteristics up to peak rate of torque development (peak velocity) are generally accepted as being independent of online corrections, i.e., representative of feedforward performance. To ensure that PF-KP, PF-KR and CF-FB groups did not make online corrections, we corroborated that the angular error at the end of each trial was similar to that at the time of peak rate of torque development (i.e., these participants produced straight cursor paths). Furthermore, for all groups we ensured that angular errors at peak rate of torque development were not dissimilar to those measured at 100 ms, i.e., this confirmed that cursor trajectories had not been modified prior to peak rate of torque development and, as such, that angular error at peak rate of torque could be as a measure 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 (after-effects) would indicate participants implemented motor commands more appropriate for the rotated task. However, accurate performance in the POST block would indicate that participants correctly implement commands for the non-rotated task. Reaction time, RT, was also 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. However, if participants adapted in a manner that required explicit decisions or compensation strategies to be implemented, pre-movement planning time would increase and result in longer RT.

Initial analysis and pilot work suggested that there were no interactions involving the eight target positions in our dependent measures. This indicates that any constraints relating to the muscle synergies involved in the required torque production did not have a significant influence on adaptation in this particular task. To characterize performance changes, a power function of the form

$$y = ax^b$$

was fitted to the cycle-averaged dependent variables for each participant within each block of trials, using a least-squares fit criteria (Newell and Rosenbloom, 1981), where  $y$  represents the value of the dependent variable on cycle  $x$ . The fitted parameter  $a$  indicates the (fitted) level of performance in the first cycle while the parameter  $b$  represents the slope of the curve, and is an indication of the rate of learning. Such power-fitting techniques have previously been used extensively in the literature (e.g., Carson et al., 2002; Hinder et al., 2007) and enable the characterization of performance throughout the learning period. They represent an alternative to approaches that focus on data obtained for the first and final trials or cycles of trials (e.g. Caithness et al., 2004). Only trials in which the target was successfully acquired were included in the curve fitting procedures for the CF-FB group (<2% trials were excluded). Furthermore, trials for all groups in which the cursor was not stationary at target presentation (i.e., if the cursor speed exceeded 15% of the maximum torque speed), and trials in which participants simply failed to move the cursor towards the target were also disregarded. These trials represent occasions where participants may have been making small adjustments to their arm posture (start location of the cursor) or short lapses in concentration. These trials numbered <1% of all trials.

Using the values of  $a$  and  $b$  we obtained a predicted value for each dependent variable for the initial and final cycle of each of the three experimental blocks, i.e., 6 fitted values (PREinitial, PREfinal, ROTinitial, ROTfinal, POSTinitial and POSTfinal) for each dependent variable for each participant. Further statistical analyses were conducted on these fitted values. Statistical comparisons of the  $b$  parameter obtained for each of the groups allowed us to assess variations in the rate of performance improvement.

To confirm that the values realised from the power-fit estimations represented the data in a similar manner to other data-reduction techniques commonly used in motor adaptation studies, we calculated the average value of each dependent variable in the first and last cycle of each trial block (PRE, ROT, POST), for each participant (c.f. Krakauer et al., 1999; Caithness et al., 2004) Statistical analyses were carried out using these values for comparison purposes only.

A two-way, i.e., 3 trial blocks (PRE, ROT, POST) × 2 times (initial, final), repeated measures ANOVA was conducted for each participant group and dependent variable. However, because of the experimental design, the main effect and interaction terms associated with the ANOVA are of no real benefit in aiding with the interpretation of the results. We do not report the main and interaction terms and, instead, focus on *planned comparisons* within the omnibus ANOVA framework. Because the comparisons we report were all *planned*, they can be reported in the absence of significant main 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 first non-rotated 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  $\alpha$  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.

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