Implicit and explicit adaptation processes during visuomotor adaptation of manual aiming movements

by

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Abstract

In this thesis I investigate how people adapt manual aiming in novel visual-motor environments and how different adaptation processes (implicit/explicit) depend on feedback type, and existing internal models (action experience). How implicit and explicit processes interact to facilitate accurate performance in adaptation paradigms is debated. One key study concluded that implicit adaptation, driven by error in expected sensory consequences, guided adaptation independent of ‘correct’ strategic/explicit processes (Mazzoni & Krakauer, 2006). We hypothesized that if these processes are independent, later explicit re-adaptation should not influence a previously acquired implicit adaptation (evidenced by unchanged after-effects).

In Experiment 1, numeric post-trial knowledge of results (KR) was used to promote explicitly-guided, re-adaptation of an implicit adaptation. Thirty participants gradually adapted aiming movements to a 30° CW visual rotation to achieve implicit adaptation (evidenced by strong after-effects). Participants practiced again with correct or incorrect (+/-15°) KR about cursor endpoint accuracy while still receiving correct cursor feedback. The incorrect KR groups showed the highest variable error, indicative of error-reducing strategic adjustments. Only the +15° error group re-adapted to KR. This resulted in larger after-effects than before KR exposure. If KR engaged only explicit processes, these results would suggest that these processes are interdependent, whereby an (implicit) internal model for aiming was updated by explicit processes, resulting in augmented after-effects. Despite existing evidence suggesting that post-trial KR facilitates only explicit adaptation, we had to test this result in our research design before concluding that the effects of KR were unique to re-adaptation. Therefore, we conducted Experiment 2 to determine whether post-trial KR could be used to update internal models for aiming without previous visual-motor experience. Thirty participants gradually adapted to a 30°

CW visual rotation receiving either concurrent or post-trial cursor feedback, or post-trial numeric KR. Although all groups showed after-effects following practice, suggesting implicit adaptation in all feedback conditions, the magnitude of after-effects was smaller for the numeric KR group. From these data we conclude that numeric KR results in both implicit and explicit adaptation and that the relative contributions of these processes to adaptation likely depends on self-attribution of errors and timing of visual feedback.

Preface

Chapters 2 and 3 contain work that was conducted under the supervision of Dr. Nicola Hodges and in collaboration with Dr. Romeo Chua. For each study, I was responsible for most of the experimental design, all data collection, data analysis, and written report of the findings.

The findings of Experiment 1 were presented at SCAPPS 2012: Making Waves Conference in Halifax, Nova Scotia.

Data collection was approved by the Behavioural Research Ethics Board at the University of British Columbia. Certificate: H09-00717.

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1. Introduction

There are instances when individuals are required to perform motor tasks in novel environments. One such example is the seemingly simple visual-motor transformation task of recalibrating the relationship between the movements of a computer mouse and the movements of the cursor on the computer screen when operating a new computer for the first time. When we perform in new environments for the first time, our movements are often quite errorful and unstable. In such scenarios, we must learn to adapt known relationships between motor commands and movement outcomes such that we can perform with minimal error in different environmental contexts. Fortunately, the human nervous system has the ability to adapt motor behaviour such that with practice, performance in perturbed environmental conditions can resemble the performance observed in “normal” environmental conditions. One well-documented proposal for how our nervous system allows us to adapt to changing environments is through the development of adaptive internal models for different motor tasks that can be recalibrated to facilitate accurate performance. In this thesis, I explore how we adapt our manual aiming movements in the presence of a novel visual rotation and importantly, how adaptation depends on (A) the type of visual feedback available, and (B) existing internal models (action experience). I am interested in the types of adaptation processes (implicit/explicit) that are engaged by different types of feedback about performance error (and internally generated error signals) and how these processes develop and interact at different stages of learning or visual-motor experience.

1.1 Adaptation learning and internal models

In the internal model framework, adaptations are thought to be achieved via an internal computation comparing an internal estimate of predicted sensory consequences for a given action and the actual sensory feedback for the movement produced (Wolpert, 1997). The resulting difference is the remaining sensory prediction error which is thought to be the teaching signal that guides motor corrections until the movement is accurate (Tseng et al., 2007; Shadmehr, Smith & Krakauer, 2010). The initial prediction of the sensory consequence of a given movement has been proposed to be generated by an internal predictor called the forward model. This forward model is informed by the context (environment and previous experience) in which the movement is performed as well as a copy of the motor command (called the efference copy) (see Shadmehr et al., 2010 & Wolpert & Ghahramani, 2000 for reviews). This forward model allows us to predict consequences of a given movement before on-line sensory feedback is available. If the predicted state (i.e. what should happen) does not match the actual state (i.e. what did happen) a sensory prediction error is generated. This informs an inverse model which can update an accurate transformation of a motor command and the sensory consequences of the movement it produced. This internal computation is believed to occur in the cerebellum as evidenced by both studies of patients with cerebellar lesions and studies using transcranial magnetic stimulation where disruption of cerebellar cortex has led to impaired state estimation processes (see Shadmehr et al., 2010 for a recent review).

Each time we are required to move in a novel environment, we must recalibrate this transformation between our predicted and actual state. The internal model framework for explaining adaptations to novel environments has been successfully applied to reaching and aiming movements (e.g. Shadmehr & Mussa-Ivaldi, 1994), human locomotion (e.g. Fortin et al., 2009), and saccadic eye movements (e.g. Ethier, Zee & Shadmehr, 2008). With respect to this thesis, we will discuss this theoretical framework with respect to targeted manual aiming. Both visuomotor and dynamic adaptation paradigms are often used to test motor recalibration (i.e.

updating of the transformation of motor command output and predicted sensory consequences) during manual reaching and aiming (see Shadmehr et al., 2010 for a review). During visuomotor adaptation (VMA), a visual perturbation is applied such that there is a mismatch between what is seen and the actual position of the hand when aiming for a target. In this case, what is seen is visually distorted but the proprioceptive feedback remains unaltered. The resulting visually-detected movement trajectory does not match with the planned movement generated by the motor command, leading to sensory prediction error. The resulting sensory prediction error can then be used to inform the inverse model to update future motor commands to improve movement accuracy. This can be achieved by having participants look through prism goggles (e.g. Mikaelian & Held, 1964) or by projecting visual stimuli onto a semi-silvered mirror that subjects are required to look at enabling computer-based alterations to cursor feedback during and after movement in the absence of vision of the hand (e.g. Bernier, Chua & Franks, 2005; Ong & Hodges, 2010). Dynamic perturbations often involve participants moving a manipulandum to a given target against an error-augmenting perpendicular force (e.g. Mattar & Gribble, 2005; Shadmehr & Mussa-Ivaldi, 1994).

In all of these adaptation paradigms discussed above, initial exposure to the perturbation results in errorful movement trajectories (i.e. inability to accurately hit the target). However, with practice, participants are able to reduce their error and improve aiming performance as a result of successful adaptation to the new environment (whether visual or dynamic). These adaptation paradigms require participants to establish a new transformation that relates their motor commands (motor output: aiming movement) to a desired sensory outcome (in this case, visual cursor feedback hitting a visual target) (Wolpert & Ghahramani, 2000).

1.2 Measurement of adaptation

Two ways that we can measure how well one has adapted to a novel adaptation environment is through tests of what have been termed direct effects and after-effects (Redding & Wallace, 1993, 2000). In the VMA paradigm, direct effects are the measure of compensatory aiming behaviour in response to the visually perturbed feedback during exposure to the visuomotor perturbation (Redding & Wallace, 1993). After-effects are measured following exposure to the visuomotor perturbation when the participant is returned to a normal environment (e.g. Held & Hein, 1958; Redding & Wallace, 1993). After-effects are proposed to provide evidence that a new visuomotor representation has been learned (Krakauer, 2009) and that an (implicit) internal model has been updated (Shadmehr & Mussa-Ivaldi, 1994; Taylor & Ivry, 2012). These effects are believed to persist because the inverse model continues to generate motor commands to compensate for the visuomotor perturbation experienced in the previous environment (Kawato, 1999). As a result, performance accuracy is unintentionally biased in the direction of the original perturbation and the normal visuomotor map of visual and proprioceptive space for aiming must be re-instated. Since the effects persist even though a participant is aware they have returned to a normal environment, after-effects are considered a strong indicator of implicit (unintentional) motor recalibration (Henriques & Cressman, 2012; Taylor & Ivry, 2013) which has also been referred to as adaptive spatial realignment (Redding & Wallace, 1993; 1996). This realignment or recalibration is not thought to involve higher level intentional processes (i.e. cognitive strategy), but rather unintentional long-latency adaptation mechanisms to realign the mapping between observed and expected movement outcomes in novel visual environments (Redding & Wallace, 1993). Traditionally, tests for after-effects have been conducted such that all visual feedback is removed (e.g. Redding & Wallace, 1993; Harris, 1974; Ingram et al., 2000; Ong & Hodges, 2010). This removes the opportunity to use on-line processing of visual feedback to accurately guide movement allowing for a more robust test of updated motor commands and motor planning processes that reflect that adaptation has occurred (Henriques & Cressman, 2012).

1.3 Explicit and implicit learning processes

Adaptation is influenced by the nature of how a perturbation is introduced as well as the degree of explicit awareness a participant has about the parameters of the task. Researchers have compared the effects of gradual introduction of a visuomotor rotation to situations when the perturbation is instantaneous (Kagerer, Contreras-Vidal & Stelmach, 1997; Ingram et al., 2000). Although both conditions result in significant after-effects, stronger after-effects are observed for groups who experience a gradual introduction of the perturbation. Unlike participants who are immediately introduced to a perturbation, gradually introduced participants are not typically aware of any systematic changes in the task during practice (e.g. Kagerer et al., 1997; Ingram et al., 2000). However, it remains unclear if explicit awareness was serving to moderate the effects of implicit adaptation or if it was simply the nature of how the perturbation was introduced that dictated the magnitude of the resulting after-effects. It is also possible for participants to adapt to an immediate introduction of a visuomotor perturbation and have limited to no explicit awareness of the direction or magnitude of the perturbation when asked in post-experiment questionnaires (e.g. Ong & Hodges, 2010; Ong, Larssen & Hodges, 2012). This may be because in the presence of large errors, some participants will rely on implicit processes to guide incremental improvements with practice rather than test strategies to reduce error immediately (Martin, Keating & Goodkin, 1996).

Explicit learning processes are cognitive in nature such that they involve conscious monitoring of movement production to achieve desired movement goals and possible awareness of the parameters of given motor task. Presence of these processes is typically evidenced by explicit strategies and hypothesis testing (Hinder et al., 2008; 2010). Explicit learning processes can be facilitated or brought about by verbal strategy/instruction about how to aim or correct error by providing manipulations to visual feedback of the movement outcome (e.g. Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011; Benson, Anguera & Seidler, 2011; Sarlegna, Gauthier & Blouin, 2007; Hinder et al., 2008). Measures of reaction time (RT) are often used to infer the implementation of explicit strategies (Benson et al, 2011; Ong et al., 2012; Hinder et al., 2010) because of the proposed increased preparation time required to implement an explicitly derived plan (i.e. less automatized than implicitly learned motor tasks). Explicit verbal instruction also typically results in immediate behavioural change when performing a VMA task (Mazzoni & Krakauer, 2006; Benson et al., 2011; Taylor & Ivry 2011). These changes are often accompanied by increased performance variability reflecting the testing of strategies after experiencing large errors when a rotation is immediately introduced.

Even though strategies have been successfully applied to improve performance (i.e., learning how to move in a rotated environment), there is considerable evidence showing that this explicitly-driven adaptation does not result in after-effects. For example, following strategically guided aiming movements in a no rotation control condition, no after-effects were seen when participants were asked to move without applying the movement strategy (Mazzoni & Krakauer, 2006). Observational practice paradigms have also been shown to encourage learning via explicitly mediated strategies. These strategic representations are learned by participants who watch videos of actors performing a VMA task before successfully performing it themselves (e.g. Ong & Hodges, 2010; Ong et al., 2012; Larssen, Ong & Hodges, 2012). Unlike actors, observers consistently report correct magnitude and direction of the rotation and the strategy used to overcome the perturbation. Importantly, they do not show after-effects immediately following observation of the rotation suggesting that self-produced movement is required for implicit adaptation to occur (see also Held & Hein, 1958).

Implicit and explicit processes have been proposed to develop simultaneously yet independently from one another during adaptation learning (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011, Sülzenbrück & Heuer, 2009). In a seminal study, participants were required to adapt to a visuomotor rotation with or without strategy information (Mazzoni & Krakauer, 2006). The group provided with an explicit strategy directing them to aim to the adjacent target in order to complete the manual aiming task accurately, immediately reduced their aiming error. However, participants were unable to maintain performance (i.e. low error) through implementation of this strategic knowledge and their aiming movements became increasingly more errorful on subsequent trials. The authors suggested that an implicit adaptation process operated independently and in parallel to adjust for the sensory prediction error generated by internal error prediction processes. Even though they correctly aimed to the adjacent target, there was still an error between the sensory feedback and the rotated cursor trajectory. It is this process that is thought to be responsible for updating of an internal model. The authors showed that this implicit process developed unintentionally and to the detriment of performance. In this case, implicit adaptation processes dominated explicitly driven adaptations.

Despite the implied independence of these processes, Benson et al. (2011) have provided evidence that knowledge of an explicit strategy can influence the magnitude of sensorimotor recalibration (as evidenced by after-effects). In their study, one group was provided with explicit information about the nature of the perturbation as well as a strategy to compensate for the visuomotor perturbation. A “no strategy” group was just instructed to aim their cursor to the target during the adaptation phase but was not provided with any explicit information. Participants that were required to employ a cognitive strategy not only had longer reaction times early in learning (reflective of increased planning time), but they had also recalibrated less compared to no-strategy controls as demonstrated by smaller magnitude of after-effects. These results are different to those of Mazzoni and Krakauer (2006), who found that the average magnitude of after-effects did not depend on explicit strategy use, reflecting an equal amount of implicit, sensori-motor recalibration independent of explicit strategic control (and both groups successfully adapted during practice to a similar degree). In contrast, Benson et al. (2011) suggest that the implementation of an explicit strategy interfered with the development of the implicit process because the explicit group recalibrated less, providing evidence that these explicit and implicit processes may in fact be interdependent, rather than independent.

1.4 Feedback and explicit adaptation.

It is possible to guide learners to achieve a given motor task with augmented feedback in the form of “knowledge of results” (KR) (Winstein & Schmidt, 1990). This information relating to movement outcome is provided after execution of a movement. In the case of VMA, KR has been provided visually, following movement completion, as a trace of the cursor trajectory of the last completed movement trial (Hinder et al., 2008; 2010; Bernier et al., 2005; Shabbott & Sainburg, 2010). When visual information is provided after movement completion, “off-line” error correction processes involving cognitive strategies are believed to be used to offset the visuomotor rotation (Shabbott & Sainburg, 2010). However, when visual feedback is provided at the same time as the movement, implicit adaptation processes are thought to be activated

(Shabbott & Sainburg, 2010; Hinder et al., 2008; 2010). Under these latter conditions, a sensory prediction error is generated that is thought to guide future movements by feedforward mechanisms proposed in the internal model framework (Shabbott & Sainburg, 2010). This suggests that in order for implicit adaptation to occur (via generation of a sensory prediction error), concurrent visual feedback must be available during movement so that concurrent comparisons can be made between visual feedback and proprioceptive inputs, resulting in the error. In contrast, delayed KR serves to encourage feedback processes that do not get incorporated into the internal model because the actual sensory feedback is not made available until after any implicit feedforward predictions are made.

There is conflicting evidence as to the effects of delayed or post-trial KR on adaptation. In a VMA paradigm, Bernier et al. (2005) demonstrated that post-trial KR can lead to implicit adaptation for manual aiming as evidenced by presence of after-effects in a no rotation, no feedback posttest. In their study, during adaptation practice, KR was provided as a trace of the participant`s cursor trajectory to the target after each aiming attempt was completed. In this task, however, the visuomotor distortion between the actual position of the participant's finger and the visual location of the cursor was introduced gradually (to a maximum magnitude of 2.5 cm). As previously discussed, gradual introduction of a rotation promotes a more implicit form of adaptation as participants are not explicitly aware of any corrections needed. Moreover, after-effects were only assessed for the straight-ahead centre target during a no rotation, no visual feedback posttest. A continuous feedback group was also assessed. Surprisingly, the magnitude of after-effects was smaller than it was for the KR group and decayed more quickly. Bernier et al. (2005) acknowledged that these findings were at odds with previous VMA literature where strong after-effects were reported after adaptation with concurrent visual cursor feedback (e.g.

Krakauer, Ghilardi & Ghez, 1999). They suggested that the participants in their study became dependent on concurrent visual feedback and less reliant on proprioception. As a result, when vision was taken away during the posttest, proprioceptive adaptation was small. Another likely explanation is that because movement times were only constrained to 400-600 ms (these movements are slow), planned changes to the initial trajectory of each aiming movement in response to the perturbation could be small and visual feedback could be used on-line to guide adaptation throughout later time points in the movement trajectory. This is possible because visual feedback can be processed in as short a time as 100 ms (Zelaznik, Hawkins & Kisselburgh, 1983). Consequently we would not expect to see full adaptation of the executed movement plan.

Despite this study showing potential re-mapping and implicit updating of internal models following provision of post-trial KR, other researchers have not replicated this effect. Rather, they have failed to show after-effects following acquisition of a novel VMA task, suggesting KR serves to engage cognitive processes based on the implementation of explicit strategies (Hinder et al., 2008; 2010). In their original study, Hinder and colleagues (2008) used an isometric force task where muscle torques measured by a transducer controlled the movement of a cursor on a screen to one of eight radial targets. Participants adapted to a 60° rotation of visual feedback. One group received continuous, concurrent visual feedback, while a second group only received visual feedback of their cursor after the completion of each trial. Only the concurrent feedback group demonstrated significant after-effects suggesting that concurrent feedback is a requirement for implicitly updating internal representations of visuomotor space. However, unlike a manual aiming task, the isometric force task did not require movement so participants were required to learn a complex transformation of isometric wrist and elbow torques to produce cursor movement on a screen. This added complexity could serve to make the task more cognitive, at least for the delayed KR group. In a follow-up experiment, participants were put through a similar protocol requiring participants to make complex two degree of freedom movements of the wrist and elbow to aim to visual targets (Hinder et al., 2010). Although this task allowed for real displacements of the effector such that participants were provided with proprioceptive feedback relating to changes in muscle force and limb position, similar results were obtained. Even though participants produced real movements, the task still required a complex transformation of elbow-wrist movement to produce cursor movement in the presence of a visuomotor rotation.

In response to these findings, Shabbott and Sainburg (2010) conducted a follow-up study to investigate if the same effects persisted in a simple manual aiming task in a VMA paradigm where a 1:1 relationship existed between movement of the hand and the cursor. Participants were required to perform manual aiming movements to one of eight radial targets and adapt aiming performance to a 30° CW visuomotor perturbation. One group received concurrent visual cursor feedback during movement while the second group only received feedback after movement completion. Presence of after-effects was assessed for both groups. Consistent with previous findings, large after-effects were reported for the continuous feedback group. The group that received post-trial feedback showed evidence of increased error during the test for after-effects, in comparison to the pretest, but these values were not statistically different. Together, these data provide support for the idea that on-line visual feedback promotes implicit adaptation. They also showed that the offline feedback engaged more explicit, hypothesis-testing strategies, as evidenced by significantly larger aiming variability throughout rotation exposure for the post-trial feedback group as well as longer RTs.

In Experiment 1 of this thesis I propose to further investigate the relationship between these explicit and implicit learning processes and to test conditions that serve to encourage adaptation learning via either of these two processes. I use the VMA paradigm with KR as a tool to encourage off-line explicit processes to see if they interfere with an implicitly developed motor plan for manual aiming.

2. Experiment 1

2.1 Introduction

This experiment was designed to address the following research question: Can an explicitly mediated learning process (encouraged by post-trial KR) alter an already implicitly acquired internal model (as evidenced by after-effects in a no-KR, no perturbation posttest)? Because of the current controversy regarding the independence of explicit and implicit adaptation processes, we designed an experiment to determine whether an implicit process could be changed through procedures designed to encourage explicitly-mediated adaptation. That is, is the implicit adaptive process independent and impervious to explicitly-mediated strategic adjustments to error?

Three different groups of participants were required to adapt targeted reaching movements to a 30° CW visual rotation. This perturbation was introduced gradually to encourage implicit updating of their internal model for aiming in a novel VMA environment. Participants received partial on-line cursor feedback (i.e. 50% of their movement trajectory) to allow for later manipulations of endpoint feedback. This implicit adaptation phase was followed by an explicit adaptation phase. In addition to the same 30° CW visual rotation of the cursor, KR was also used as a tool to encourage off-line explicit processes and implementation of an explicit strategy. At this point, all groups received a different KR manipulation that was either the actual numeric value of their aiming accuracy in the VMA environment (correct KR), or an erroneous error score that was implemented to bias future reaching movements in either the clockwise (CW, KR-15°) or counterclockwise (CCW, KR+15°) direction relative to the target. The 15° value for the erroneous KR groups was selected because it was a large enough difference to allow inferences about its effect and was the reported just noticeable difference (JND) detection threshold for attributing errorful movements to oneself reported in a study of VMA to a cursor rotation (see Synofzik, Lindner & Their, 2008). Each of the respective adaptation phases was followed by a test of after-effects. Presence of unintentional after-effects served as an indication that implicit updating of an internal model had occurred.

We predicted that if these two processes are independent, we would not expect any significant change in the magnitude of after-effects following the provision of erroneous post-trial KR. However, what we found was a change in the magnitude of after-effects following exposure to erroneous post-trial KR for the KR+15 group only. This suggests that these processes are not independent and that an explicitly-mediated control strategy (in the presence of a CW visuomotor perturbation) was incorporated into a previously acquired internal model for reaching.

2.2 Methods

2.2.1 Ethics statement

All procedures were conducted according to the regulations of the Behavioural Research Ethics' Board of the University of British Columbia. Written informed consent was obtained from all participants.

2.2.2 Participants

Thirty, naïve, self-reported right-hand dominant participants were randomly allocated to 3 groups (n = 10/gp) who differed depending on the type of KR provided in the second adaptation phase. A correct KR group (KR) received correct numeric post-trial KR of their reaching accuracy and two separate erroneous KR groups received post-trial KR that augmented their actual performance error by 15° promoting either CCW (KR+15°) or CW (KR-15°) aiming of the index finger relative to the actual cursor trajectory which was already rotated 30° CW.

2.2.3 Task and apparatus

Participants performed right-hand aiming movements with a custom mouse connected to a graphics' digitizing tablet (Calcomp Drawing Board IV, 200Hz). The mouse had a plastic extension with a central crosshair whose coordinates were registered by the tablet. All participants were asked to centre the index finger of their right hand on this crosshair. Aiming movements were made to 5 equally-spaced visual targets that were projected onto a semi-silvered mirror positioned between the participant's line of vision and their hand in the workspace. The central home position was a 0.6 cm X 0.6 cm square. The radius from the centre of the home position to the centre of each target was 9.5 cm. Target and cursor diameter were both 0.4 cm. The participant's head was supported by a chin rest positioned just outside of the workspace. The distance between the chin rest and the central home position was 26.5 cm (see Figure 1 for diagram of set-up).

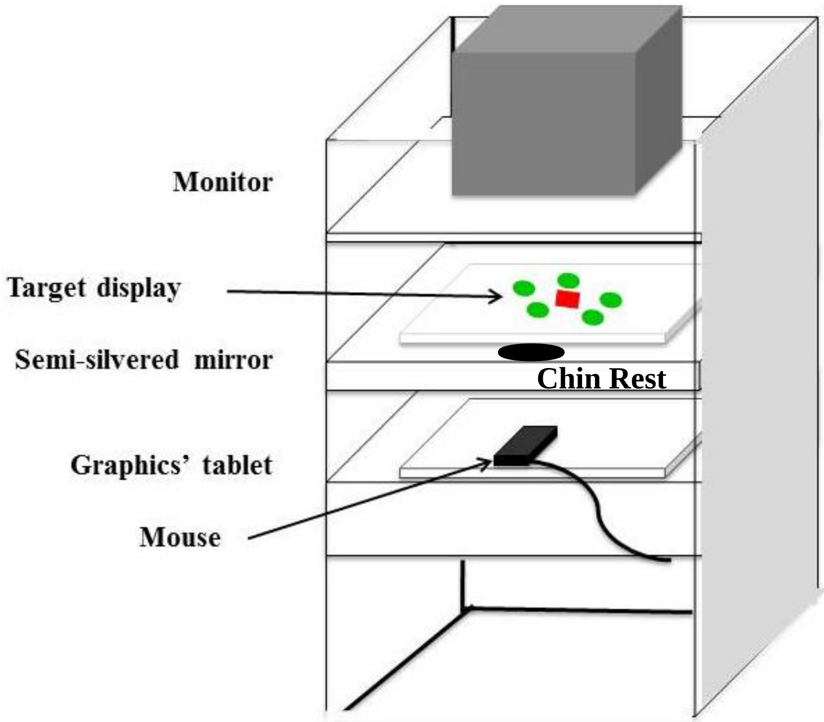

Figure 1. Visuomotor adaptation set-up.

2.2.4 Procedure

Procedures were similar to those adopted in previous studies (e.g. Ong et al., 2012). For a summary of experimental conditions, see Table 1.

Group	Pre-test (normal)	Adapt1 (30°CW – gradual)	After-effects1 (normal)	Rotation Awareness (Pen & Paper)	Adapt2+KR (30°CW – immediate)	After-effects2 (normal)	Rotation Awareness (Pen & Paper)	Retention (30°CW)	Explicit Awareness Questionnaire
KR (n=10)	All t=20 No CT No KR	All t=100 ½ CT No KR	All t=20 No CT No KR	All	t=100 ½ CT Correct KR	All t=20 No CT No KR	All	All t=20 No CT No KR	All
KR+15 (n=10)					t=100 ½ CT Incorrect KR (error + 15°)				
KR-15 (n=10)					t=100 ½ CT Incorrect KR (error-15°)				

KEY:
All: all groups performed this condition
t: trials
FB: visual feedback
CT: cursor trajectory
KR: Knowledge of Results

Table 1. Procedures for all experimental conditions to be experienced by the 3 groups in Experiment 1.

All groups performed a pretest to provide a baseline measure of normal aiming without any visual feedback. Targets were presented randomly to prevent the participants from anticipating future target positions. They were asked to perform fast shooting movements through the target as soon as the target appeared. Shooting movements are different from pointing movements in that the participant does not have to terminate their aiming movement inside the target which would otherwise slow down movement times (Tseng et al., 2007). It has been proposed that shooting movements rely on sensory prediction errors for adaptation because they are typically faster than pointing movements, which reduces the opportunity for on-line motor corrections (Tseng et al., 2007). After each aiming trial, participants moved the cursor back to the central home square, however vision of the cursor was not made available until they were within 4.75 cm of the central home position. A new target was presented after the cursor was inside the home square for 1.5 s.

The pretest was followed by initial exposure to the VMA environment (Adapt 1; 30° CW rotation) where online cursor trajectory was rotated 30° CW relative to actual hand position. No group-based manipulations occurred in this first adaptation phase. Only the first 50 % of the cursor trajectory trace from the centre position to the target was visible during this phase so that endpoint KR could be manipulated when provided during the second adaptation phase. The visuomotor rotation was gradually increased by 5° CW every 5 trials up to a maximum of 30° CW such that participants finished this adaptation phase with 75 trials of practice in the 30° CW environment. This method of gradual adaptation has successfully been implemented by others and leads more reliably (than immediate introduction) to implicit (unaware) adaptation (e.g. Klassen, Tong & Flanagan, 2005). We then tested for after-effects (Posttest1). Participants were informed that they had returned to a normal environment although they did not receive visual feedback of the cursor. The rationale for telling all participants that they had returned to a normal environment (following the implicit adaptation phase) was that if after-effects were still present, we could make a stronger case that the adaptation effects seen were indeed unintentional (i.e., implicitly mediated). They were once again asked to perform accurate aiming movements through the targets as quickly as possible. After this first test of after-effects participants' explicit awareness of the visuomotor rotation implemented during Adapt 1 was assessed. This was conducted as a manipulation check to determine whether or not participants were aware of the presence of the rotation (recall that awareness has been shown to moderate magnitude of after-effects). This was achieved using a pen and paper test (see Figure 2 below). Participants were told to assume that the black lines represented an accurate cursor trajectory for aiming. They were then asked to draw the trajectory that their right index finger would have had to follow to produce the same cursor trajectory depicted by the diagram.

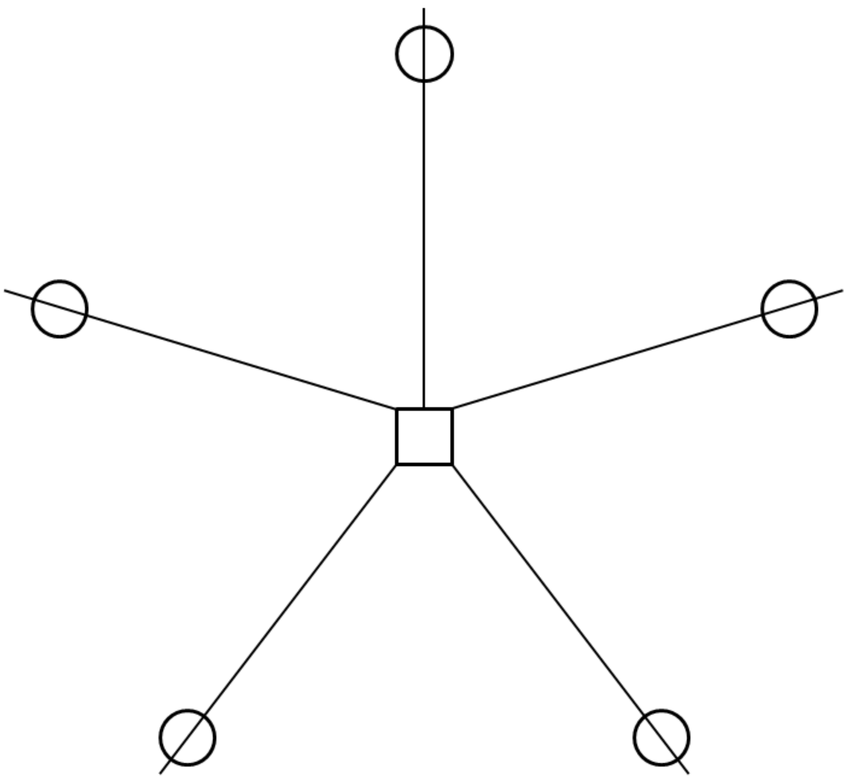

Figure 2. Schematic diagram of target array and home position for accurate cursor trajectories that was presented to participants during assessment of rotation awareness. Distance between centre of home square and centre of each target was 9.5 cm (same as VMA task).

This assessment of explicit awareness was followed by the second phase of adaptation where our group manipulation took place. Participants continued to perform aiming movements with their cursor rotated 30° CW relative to their index finger and hence the rotation was introduced immediately on the first trial. In addition to half the online cursor feedback, the groups received their respective post-trial KR manipulations in the form of a numeric error score.

This KR was provided off-line immediately after the cursor exceeded 9.5 cm which was the radius of the circle that subtended all 5 targets. The KR appeared beside the intended target on a blank screen as a positive or negative value after each trial. Participants were informed on 2 occasions (before the start of Adapt2 and after completion of 50 trials) that negative scores indicated error (in degrees) in the CCW direction of the cursor relative to the target, positive scores indicated error in the CW direction between the rotated cursor and the target, and a score of zero (0°) indicated that the participant accurately hit the target. They were instructed to use this error information about the magnitude and direction of their performance error to achieve an error score of 0° for each target. At this time, participants were also provided with a compensatory strategy to correct their movements based on their KR feedback. For example, participants were told that if they received a negative value, they were to adjust their aiming movements by moving in the CW direction. Participants were never told whether or not the numeric KR was erroneous.

A final test of after-effects (Posttest2) was conducted followed immediately by a second test of explicit awareness of the rotation experienced during Adapt2 (same procedure as previous). This was then followed by a retention test of the 30° CW rotation. During this retention test, participants once again only received online visual feedback of the first 50 % of the visual trace of their cursor trajectory. Participants were asked to aim using the same strategy that they used to get their KR to 0° during Adapt 2 but they were not provided with post-trial KR of their aiming performance.

After experimental testing, a final assessment of explicit awareness of the adaptation conditions was conducted to determine if the KR provided during Adapt2 was believed to be attributed to self-produced movement. This was included to control for differences that may be attributable to "believability of KR" and potentially exclude participants who did not attempt to make changes to their reaching movements in response to the post-trial KR (See Table 2 for full debrief questionnaire adapted from Benson et al., 2011).

Question	Response
(1) Did you notice the task get harder at any point?	If **YES**, when? → Record Response: proceed to **(2)**. If **NO**, proceed to **(3)**.
(2) Do you know why it became harder?	**ROTATED**, proceed to **(4)**. **OTHER/NO**, proceed to **(5)**.
(3) Did the cursor move where you intended it to?	If **YES**, proceed to **(6)**. If **NO**, proceed to **(2)**.
(4) How many degrees was the cursor rotated?	Record Response:
(5) What did you do to correct for it?	**ROTATED FEEDBACK**, proceed to **(4)**. **OTHER**→Record Response:
(6) When you received error score during Adapt2, did this score accurately show your reaching error?	**YES** **NO,** proceed to **(7)**
(7) If you answered NO to (6), what was different about the FB with respect to your actual movement trajectory?	Record Response:

Table 2. Questionnaire of explicit awareness of rotation and erroneous KR provided in Adapt2. Adapted from Benson et al. (2011).

2.2.5 Measures and analyses.

The primary dependent variable of interest was directional constant error (in degrees) from the target measured at peak tangential velocity of the movement trajectory. This method has been used in previous experiments and peak velocity occurs consistently at approximately 75% of the distance to the target (e.g. Larssen et al., 2012; Bernier et al., 2005). A positive or negative value for error denotes a CW or CCW error respectively. Reaction time (RT) data were also collected as a measure of movement planning. Previous work suggests that the implementation of explicit strategies slows reaction times relative to acquisition by more implicit means (e.g. Hinder et al., 2010; Benson et al, 2011; Larssen et al., 2012). Reaction time was calculated from the time of target presentation to movement onset. Movement onset was defined as the point in time when the cursor left the central home square. Variability in aiming accuracy (standard deviation of constant error in degrees) was also calculated as an indirect measure of explicit strategy use. More variable performance has been linked to implementation of cognitive strategies (Shabbott & Sainburg, 2010). Aiming trials where movement time (MT) exceeded 300 ms were excluded from analyses to control for potential on-line corrections. Aiming trials where reaction times exceeded 1000 ms were also excluded from analysis. This resulted in a mean exclusion of 3.9% of the total trials executed by all participants (KR = 3.8%, KR+15 = 3.8%, KR-15 = 4.2%).

Mixed-factor analyses of variance (ANOVA) were conducted with Group (KR, KR+15, KR-15) as the between-subject factor. Repeated measures were conducted on the remaining factors: Phase (Pretest vs Posttest1 vs Posttest2, or Adapt1 vs Adapt2), and Block (2 or 10). Partial eta squared (η_p^2) values are reported as measures of effect size. Post-hoc analyses were conducted using Tukey HSD (p<0.05) and Greenhouse-Geisser corrections to *df* were applied for violations to sphericity.

2.3 Results

2.3.1 Evidence for gradual adaptation during the implicit adaptation phase

As illustrated in Figure 3, all 3 groups improved performance accuracy over the last 7 blocks of practice during Adapt1. This was evidenced by a significant block effect $F(5.138, 138.72) = 51.22$, $p < 0.001$, $\eta_p^2 = 0.66$. Initial increases in CE (during the first 3 blocks of practice) can be attributed to the step-wise increase in the magnitude of the perturbation which was not at its maximum (30° CW relative to mouse/finger position) until the last 5 trials of Block

3. All groups had similar performance which was expected because they had performed in identical practice conditions during this implicit adaptation phase. There was no group main effect $F(2, 27) = 1.65$, $p = 0.21$, $\eta_p^2 = 0.11$, and no Group X Block interaction $F < 1$.

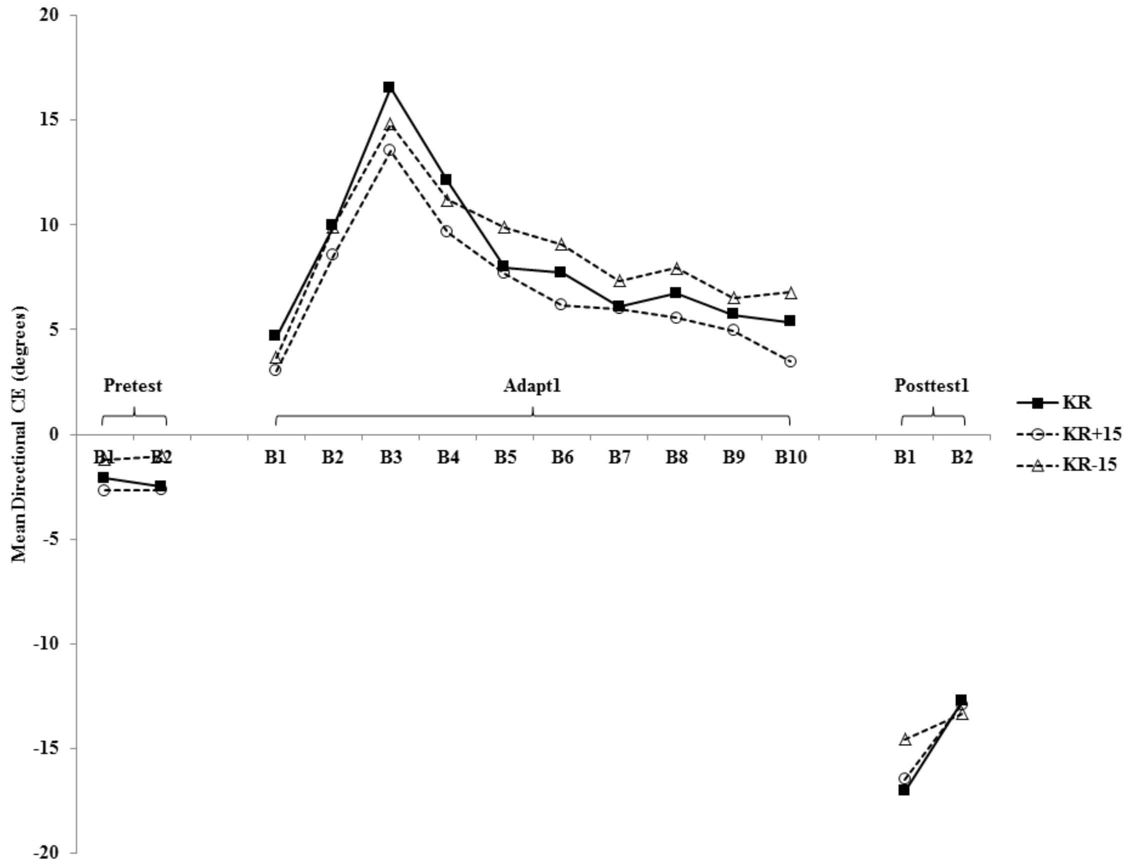

Figure 3. Mean directional CE of cursor trajectory reported as a function of Block (B) during the Pretest, implicit adaptation phase (Adapt1), and first test of after-effects (Posttest1). A positive value means that error was in the CW direction relative to the intended target. Rotation was turned off during pretest and posttest. Full 30° CW visuomotor perturbation begins during Block 3 of Adapt1.

2.3.2 Evidence for strong after-effects following gradual adaptation

Performance error (CE) for all groups during the pretest and the first posttest is illustrated in Figure 3. As would be expected, there was no significant main effect of group $F(2, 27) = 1.39$, $p = 0.27$, $\eta_p^2 = 0.09$, and no significant Group X Phase ($F < 1$) or Group X Block interactions

$F(2, 27) = 1.08$, $p = 0.35$, $\eta_p^2 = 0.07$. Following the implicit learning phase, all groups had increased CE in the counterclockwise (CCW) direction indicating the presence of after-effects. This was evidenced by a main effect of phase, $F(1,27) = 610.02$, $p <0.001$, $\eta_p^2 = 0.96$. The magnitude of after-effects diminished for all groups by the second block as evidenced by a significant block effect, $F(1, 27) = 14.96$, $p = 0.001$, $\eta_p^2 = 0.36$ and a Phase X Block interaction, $F(1, 27) = 20.00$, $p < 0.001$, $\eta_p^2 = 0.43$, due to the greater reduction in Posttest1.

2.3.3 The KR manipulation successfully moderated aiming accuracy during the explicit adaptation phase

During this second adaptation phase, the 3 groups were provided with endpoint KR about their aiming error which they could use to adjust future movements.[1] CE was calculated relative to the 30° CW cursor rotation and hence errors in Figure 4 are closer to zero for the correct KR group and in the direction of the erroneous terminal KR provided for the KR +15 and KR-15 groups. Both erroneous KR groups were able to use the terminal KR to guide their aiming movements in the presence of a 30° CW visuomotor rotation to their on-line reach trajectory. As can be seen in Figure 4, the KR+15 group adjusted to the erroneous KR more that the KR-15 group across practice blocks. There was a significant main effect of group, $F(2, 27) = 29.98$, $p <0.001$, $\eta_p^2 = 0.69$. Only the KR+15 group was significantly different (more errorful) than the correct KR group ($p < 0.001$). There was also a significant Group X Block interaction, F(10.18,

[1] A fourth group (n = 5) of participants was later tested with no KR throughout both adaptation phases (No KR) to control for any potential effects of KR during Adapt2. The Correct KR group and No KR control group had similar CE to each other during Adapt2 suggesting that there were no effects due to the mere presence of post-trial KR (Correct KR, $M = 5.7°$, $SD = 2.8°$; No KR, $M = 5.7°$; $SD = 2.3°$). We conducted a separate 2 Group X 10 Block ANOVA for Adapt2 CE and found that the means for correct KR group were not different from the means of the No KR group. There was no significant main effect of group or a Group X Block interaction (both Fs < 1).

137.39) = 8.64, $p < 0.001$, $\eta_p^2 = 0.39$. As can be seen from Figure 4, the change in error across blocks was most notable for the KR+15 group who continued to show a change in error at least until block 8 in practice (whereas there was little change in error for the other 2 groups from B3 onwards).

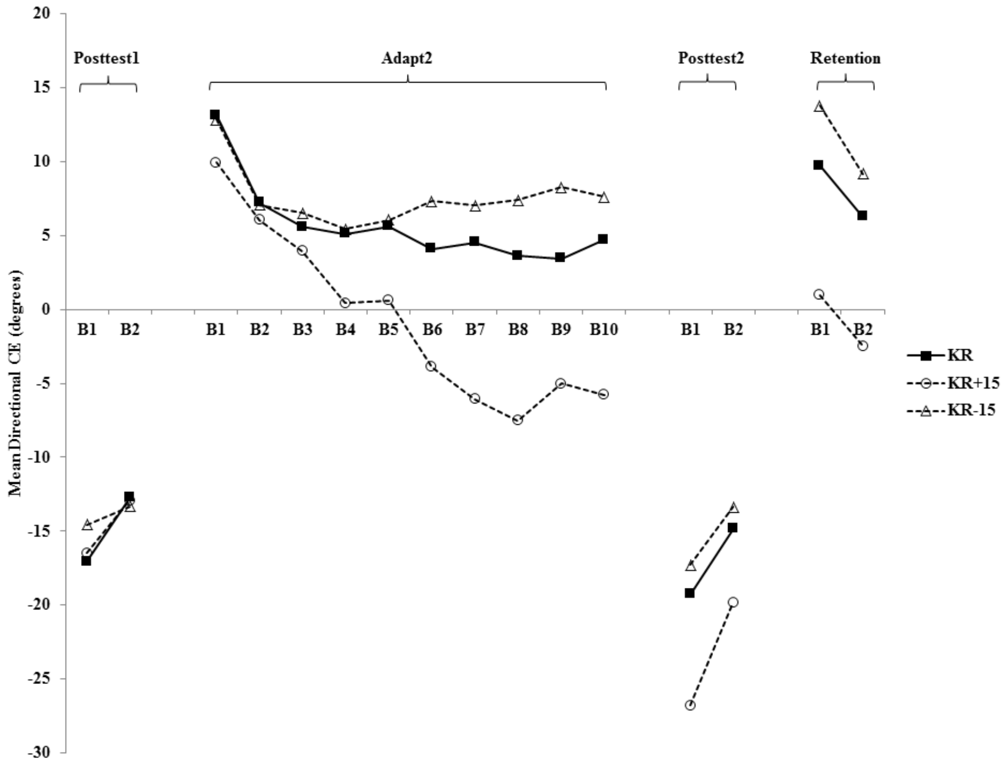

Figure 4. Mean directional CE of cursor trajectory reported as a function of Block (B) during the first test of after-effects (Posttest1), the explicit adaptation phase (Adapt2), the second test of after-effects (Posttest2), and Retention test. There was no rotation during both posttests. A negative value means that error was in the CCW direction to the intended target. A 30° CW visual rotation was introduced immediately during Adapt2 and Retention phases. The KR-15 group was aiming for +15° target error and the KR+15 group was aiming for a -15° target error.

2.3.4 After-effects covaried with the KR manipulation: Evidence of implicit adaptation following explicit manipulation of target error

Performance error (CE) for all groups during the first and second test for after-effects is illustrated in Figure 4. Following the explicit adaptation phase (i.e. Adapt 2), errors increased in the counterclockwise (CCW) direction relative to Posttest1. This was evidenced by a significant main effect of phase, $F(1, 27) = 18.98$, $p < 0.001$, $\eta_p^2 = 0.41$. There was also a significant group effect, $F(2, 27) = 4.13$, $p = 0.027$, $\eta_p^2 = 0.23$, and a Group X Phase interaction, $F(2,27) = 6.07$, $p = 0.007$, $\eta_p^2 = 0.31$.The KR+15 group was statistically more errorful than both the correct KR and KR-15 groups (*ps* < 0.05), however there was no difference between the KR and KR-15 groups. As seen in Figure 4 and evidenced by the interaction, these group differences were only seen in Posttest2 and only the KR+15 group showed a significant increase in CE from Posttest1 to Posttest2.

2.3.5 The KR manipulation led to an explicitly mediated mode of acquisition

(i) Variable error

Measures of mean variable error of aiming accuracy (VE) as well as measures of reaction time (RT) were also taken to inform as to the processes involved in adapting to terminal KR. Both measures have been reported for all 10 blocks of the implicit (Adapt1) and the explicit (Adapt2) adaptation phases. When post-trial KR was introduced during Adapt 2, VE increased for all groups (see Figure 5) as demonstrated by a main effect of testing phase, $F(1, 27) = 11.27$, $p = 0.002$, $\eta_p^2 = 0.29$. There was also a significant Group X Phase interaction, $F(2, 27) = 6.86$, $p = 0.004$, $\eta_p^2 = 0.34$. Post-hoc analysis revealed that mean VE of the KR+15 group during Adapt2 was statistically different from the means of the other 2 groups ($p < 0.05$) who did not differ from each other. The 3 groups were not different in Adapt1. There were no other statistically significant effects.

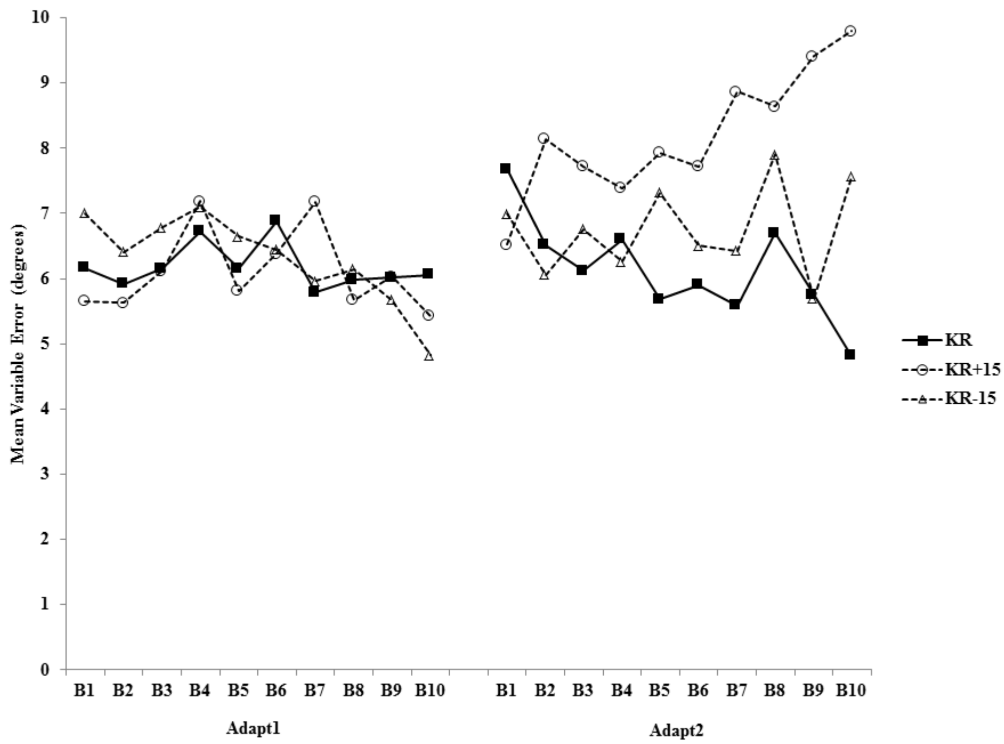

Figure 5. Mean Variable Error (VE) of manual aiming accuracy (i.e. SD of mean CE) reported as a function of Phase (Adapt1 or Adapt2) and Block (B) for all groups.

(ii) Reaction time

Despite the fact that this was not an RT task, RT values increased for both erroneous KR groups during the explicit adaptation phase reflecting strategic planning of future movements (see Fig 6 for RT data). Although all interactions were statistically significant, we were most interested in the effects between group and phase because this is where we implemented our primary manipulations. RT increased for all groups from Adapt 1 to Adapt 2, which was evidenced by a significant effect of phase, $F(1, 27) = 82.69$, $p <0.001$, $\eta_p^2 = 0.75$. This effect, however, was dependent on group, $F(2, 27) = 17.53$, $p <0.001$, $\eta_p^2 = 0.57$. Mean RT for the KR+15 group during Adapt2 was statistically slower than the mean RTs for the other 2 groups. The groups did not differ in Adapt1. A 3-way interaction was also observed due to the variability in RTs across block during Adapt2 as a function of group, $F(10.04, 135.49) = 2.03$, $p = 0.034$, $\eta_p^2 = 0.13$.

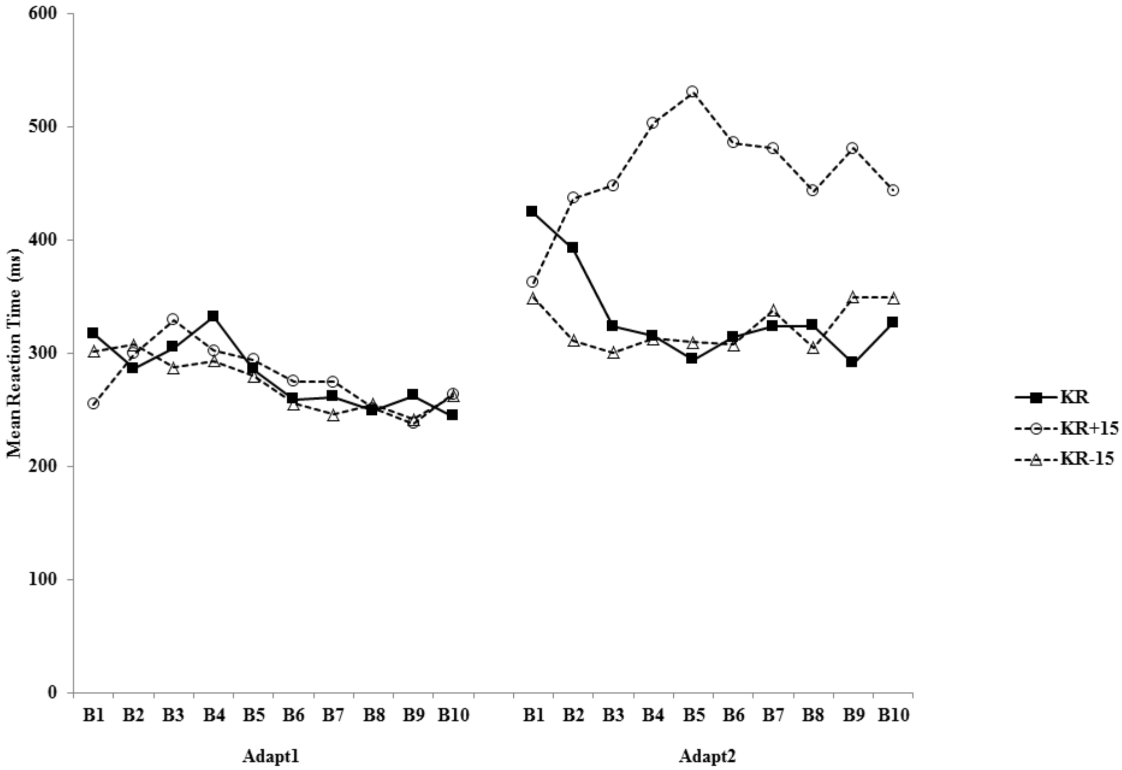

Figure 6. Mean reaction time (ms) reported as a function of Phase (Adapt 1 or Adapt2) and Block (B) for all groups.

(iii) Explicit knowledge assessment

Explicit awareness of the 30° CW visual rotation of the cursor trajectory was assessed at 2 different times following each test of after-effects. The estimated size of the cursor rotation is given in Table 3 along with between-target variability (SD) and the number of people who consistently reported the correct direction of the rotation for all 5 targets. Following Adapt1, only 2 out of 30 participants correctly reported the direction of the visual rotation suggesting that adaptation to the perturbation was not contaminated by a strategy that may have developed as a result of awareness. Following Adapt2, this had increased marginally to n=4/30 (2 participants in the KR correct group and 2 in the KR+15 group). Recall that we had gradually (implicitly) adapted participants to this 30° CW rotation so we did not expect group differences with respect to awareness of the original rotation.

Inspection of the mean estimated angle of rotation for the 3 groups in Adapt1 confirmed that participants showed little to no awareness of the 30° CW rotation, reporting differences between their hand and the cursor of between 0 and 2.1° on average. After Adapt2 there was some increase in the reported size of the rotation, particularly for the KR+15 group. However, a 3 Group X 2 Phase ANOVA on the estimated size of the rotation from the target diagrams did not yield a statistically significant effect of phase, $F(1, 27) = 1.91$, $p = 0.18$, group $F(2, 27) = 1.22$, $p = 0.31$, nor a Group X Phase interaction, $F < 1$. There were also no significant effects with respect to the variability of their estimations (all *Fs* < 1).[2]

	Adapt1 (+30°, clockwise)			Adapt2 (+30°, clockwise)		
Group	Dir (n)	Size (M)	Size (SD)	Dir (n)	Size (M)	Size (SD)
KR	1	0.07 (8.93)	7.63 (6.47)	2	1.36 (8.48)	6.64 (3.67)
KR+15	1	0.93 (3.49)	4.23 (4.94)	2	6.56 (15.28)	5.48 (5.55)
KR-15	0	-2.14 (8.14)	6.71 (5.30)	0	-1.66 (8.51)	6.62 (5.40)

Table 3. Number of participants (out of 10) who consistently reported (on schematic diagrams of the target display) the correct direction (Dir) of the visual rotation of the cursor for all 5 targets during Adapt1 and Adapt2. Mean estimated angle of the rotation of the cursor measured from the diagrams (M) and mean between target standard deviation (SD) are reported in degrees (°) across all 5 targets. Between-subject SDs are reported in parentheses for each measure.

[2] Despite not being able to correctly identify the direction of the visuomotor rotation, 8, 5, and 8 (out of 10) participants in the KR, KR+15, and KR-15 groups respectively, reported feeling like the cursor trajectory did not accurately map onto the movement trajectory of their index finger. Separating Rotation-Aware versus Rotation-Unaware participants during analysis did not result in any statistically significant group differences. Additional analyses looking at KR-Aware and KR-Unaware also failed to show any statistically significant group differences with respect to CE measures.

Following testing, a final interview was conducted to assess awareness of the rotation and the KR manipulation. As expected, all participants in the correct KR group attributed the KR as being an accurate representation of their aiming error. In the KR+15 and KR-15 groups, 8 and 7 participants respectively (out of 10) reported that the KR received was not an accurate representation of their aiming error. These 8 participants in the KR+15 group reported that they attempted to apply a corrective strategy by aiming in a more CCW direction to achieve an accuracy score of 0°, however only 4 of the 7 participants in the KR-15 group that were aware that the KR was erroneous, reported applying a corrective strategy to reduce errors. Although these participants reported being aware that the KR was erroneous, when asked, all participants reported that they still attempted to reduce their KR error score to 0°, even though it was not congruent with the position of the cursor.

2.3.6 Retention performance

A separate analysis of retention was conducted to examine the success of the strategic adjustments used during Adapt2 in the absence of post-trial KR. These data are again depicted in Figure 4. Like the acquisition data at the end of Adapt2, the KR+15 group continued to show error in the CCW (more negative) direction relative to the other groups. Although there is evidence of forgetting due to interference from performing in Posttest2 (i.e. error increased), group differences remained which was evidenced by a significant group effect, $F(2, 27) = 13.69$, $p < 0.001$, $\eta_p^2 = 0.50$. Only the means of the KR+15 group were different from the KR ($p = 0.003$) and KR-15 ($p < 0.001$). There was a significant block effect, $F(1, 27) = 30.72$, $p < 0.001$, $\eta_p^2 = 0.53$, which reflects the reduction in error across block for all groups. There was no significant interaction ($F < 1$)

2.4 Discussion

In Experiment 1, participants successfully adapted aiming movements in the presence of a gradually introduced 30° CW visual rotation. We believe that this was achieved implicitly as evidenced by an absence of correct awareness of the nature of the rotation in 28 out of 30 participants in addition to strong after-effects in the first posttest. In the second adaptation phase, participants, at least in one of the groups, were able to guide aiming movements using endpoint KR that was provided after movement completion. Erroneous KR in the form of an additional 15° CW rotation encouraged explicitly-driven adaptation as evidenced by increased reaction times and increased aiming variability throughout practice, consistent with implementation of a strategy. Significantly larger after-effects were reported for the KR+15 group during the posttest following the KR manipulation, however the KR-15 group did not demonstrate any difference in after-effects from the correct KR group.

These data provide evidence that erroneous terminal KR can alter the adaptation of an implicitly acquired rotation, updating a previously acquired internal model. This would suggest that explicitly-driven adaptation can interact with implicitly-driven processes to update a motor plan and produce unintentional after-effects. As such, explicit and implicit processes appear to show interdependence, rather than independence as suggested by Mazzoni and Krakauer (2006).

Limits

At present it remains unclear if the explicitly-driven adaptation during Adapt2, which ultimately led to increased after-effects for the KR+15 group only, was modifying the existing implicitly acquired internal model for aiming in the presence of a 30° CW visual rotation or if implicit processes were also working concurrently to update the internal model in response to the

KR. This second scenario would be possible if post-trial feedback does lead to after-effects (see Bernier et al., 2005).

We are also not certain why the KR+15 showed significantly different adaptation effects from the KR-15 group. This result may be due to the fact that KR-15 feedback encouraged participants to re-adapt in the direction of a no-rotation/veridical mapping between the hand and the cursor, which might be more difficult than augmenting an already acquired rotated strategy by 15° (i.e. +15° CW). However, we are not aware of any literature that would support such a conclusion. Compared to the correct KR group, the KR-15 group seemed unable (unwilling) to adjust their aiming accuracy even though this would have brought them closer to “normal” aiming and the KR score closer to zero. Surprisingly, even with off-line terminal KR available, the correct KR group did not improve their aiming such that their KR error score approximated 0° more consistently. Examination of the last 2 blocks of Adapt 2 (Figure 4) shows that both the KR+15 and KR-15 groups were an equal distance (+/- 7°) from 0°, which also represents reach error for the correct KR group. This would signal that all groups were attempting to achieve their explicit goal, yet only the KR+15 group’s performance was reflected in after-effects that were significantly different from the correct KR group. Perhaps we are more sensitive to increasing error in the direction of the initial CW perturbation, such that increased error values are indicative that further adaptation is required, whereas any changes in the error signal as a result of the KR-15 feedback gets ignored and/or coded as noise associated with normal performance variability (recall that aiming variability for the KR-15 group only deviated from the KR group late in Adapt2).

Another trend of interest between the two erroneous KR groups is the shift in CE back to 0° for the KR+15 group during the last 2 blocks of Adapt2. This could potentially be evidence of competition between independent explicit and implicit processes as the implicit process (bringing error closer to the implicitly acquired internal model) kicks in to override explicit control (similar to Mazzoni & Krakauer, 2006). Given the limited number practice trials, it is difficult to say whether or not the implicit process would take over and aiming error would eventually go to 0°, or if explicit and implicit processes would continue to compete as one explicit error signal (from the post-trial KR) encourages one direction of movement, while the sensory prediction error continues to drive the implicit process to achieve a different target error goal (e.g. Taylor & Ivry, 2011).

In summary, from Experiment 1 we have shown that information from erroneous KR can be integrated in and update an existing, implicitly acquired internal model for aiming movements. These findings are at odds with previous literature and the suggestion that implicit adaptation processes are impervious to concurrent, explicitly driven strategies (e.g. Mazzoni & Krakauer, 2006). This raises the question as to whether newly acquired implicit models for aiming can be updated by explicitly driven strategies but that models for normal aiming cannot. It was therefore necessary to first confirm that post-trial feedback does not lead to updating of internal models for aiming in the absence of any previous practice experience as has been demonstrated in past research (Hinder et al., 2008: 2010; Shabbott & Sainburg, 2010).

3. Experiment 2

3.1 Introduction

In Experiment 1, we showed that an explicit learning manipulation led to the updating of an existing internal model for manual aiming (i.e. an implicit process) in a novel visual motor environment. This was evidenced by an increased magnitude of after-effects following exposure to an erroneous KR signal. However, before we could make any definitive conclusions about the processes underpinning these effects we needed to confirm that post-trial KR does not actually result in after-effects. Although there is significant evidence that it does not (Hinder et al., 2008; 2010) or results in after-effects of significantly reduced magnitude (Shabbott & Sainburg, 2010), there is some reason to question these findings. Therefore, the purpose of Experiment 2 was to confirm whether or not post-trial feedback (visual cursor and numeric KR) results in after-effects when participants have no previous adaptation experience aiming in the presence of a visual rotation.

Recall that in the studies by Hinder and colleagues, participants performed a VMA task where they were either provided with concurrent cursor feedback while they were aiming, or with the trace of their cursor trajectory after the movement was completed. The concurrent feedback group was further divided into participants who were allowed to make on-line corrections to their aiming trajectory, and participants who were not. The group receiving post-trial KR of the cursor trajectory was asked to produce fast uncorrected torques to achieve a spatial target position. Although all groups adapted during practice by successfully minimizing aiming error, only the concurrent feedback groups showed after-effects. In addition, on-line corrections did not moderate the magnitude of after-effects in the concurrent feedback group. In their first study, participants produced isometric flexor-extensor/supination-pronation torques to produce cursor movement (Hinder et al., 2008). In a second study movement was not constrained, such that movement of the wrist and forearm controlling a handle, produced cursor movement on a computer screen (Hinder et al., 2010). The task required participants to adapt both wrist and elbow coordination in order to accurately aim a cursor to different visual targets on a computer screen in the presence of a visual rotation. The lack of direct correspondence between the effectors and the visual output might have encouraged a greater reliance on the visual feedback of the cursor than typically seen in VMA tasks. Since the KR group only received visual feedback of their cursor trajectory after the movement was completed when their hand was back to the starting posture, it is unlikely that participants were able to make any meaningful comparisons between the wrist and elbow torques needed to be generated (Hinder et al., 2008) or the perceived position of their forearm (Hinder et al., 2010) because error information was only provided while they were at rest. This would put greater demands on working memory as participants would be required to recall the parameters of their previous action and relate it to the delayed visual feedback resulting in a strategically-driven mode of control.

Shabbott and Sainburg (2010) used a similar set-up to the one used in Experiment 1of this proposal and also noted an absence, or at least significantly reduced after-effects following adaptation with post-trial KR. This was again in comparison to two different groups that received concurrent visual feedback of their cursor trajectory during aiming that were either allowed to make on-line corrections during aiming or were asked to make uncorrected movements. In this study and those of Hinder and colleagues there was evidence (via RT, VE and explicit strategy recall measures) that post-trial KR prompted explicitly-driven adaptation that prevented or at least moderated implicit adaptation and updating of motor commands. Across studies, the magnitude of the initial direction of the after-effects did not differ between participants who received concurrent cursor feedback and either were or were not allowed to make on-line corrections, suggesting that motor corrections do not facilitate or inhibit implicit adaptation.

Despite researchers showing a lack or reduced after-effects as a result of post-trial KR, Bernier et al. (2005) observed stronger after-effects when post-trial KR was provided in comparison to concurrent feedback. In this study, there were only two horizontally presented targets and the rotation was introduced gradually during adaptation. It is possible that this gradual introduction of the rotation could have moderated the effects of KR. By introducing a perturbation gradually, participants are typically unaware of a discrepancy between their actual hand position and the visual feedback of their cursor (small increases in error, less than a 15° rotation, seems to make participants attribute errors to self-generation, Synofzik et al., 2008). This type of gradual adaptation protocol has led to larger magnitude of after-effects compared to protocols where participants are immediately introduced to a visual rotation (Kagerer et al., 1997; Ingram et al., 2000). Due to this discrepancy in findings about the role of post-trial KR in VMA paradigms, with respect to the type of adaptation process, there is a need to ensure that the post-trial KR-related effects (in Experiment 1) were due to explicitly-driven processes and that after-effects (indicative of more implicitly-driven learning) are not seen in the absence of previous experience with this task.

In the second experiment of my thesis, participants adapted to a 30° CW visual motor rotation with either concurrent cursor trajectory feedback (on-line) or post-trial feedback. Post-trial feedback was provided as a visual cursor trajectory for one group (as has been done in previous studies) or as a numeric error score (knowledge of results, KR) pertaining to target error (in degrees, same as Experiment1). To our knowledge, the only work that has been conducted using post-trial numeric feedback to guide manual aiming movements was in non-rotated environments, where researchers compared endpoint accuracy and within-subject aiming variability between participants that received concurrent cursor feedback versus different types of post-trial KR (e.g. Bernier, Chua, Franks & Khan, 2006). Erroneous KR has been studied in a coincident anticipation timing task, where it was shown that participants will use erroneous KR even if it conflicts with their own correct intrinsic feedback (Buekers, Magill & Hall, 1992). This suggests that erroneous augmented numeric feedback can be used to successfully bring about learning even when it potentially conflicts with veridical (proprioceptive) feedback about accurate aiming.

Consistent with previous findings, we expected all groups, regardless of the type of feedback, to successfully adapt to the visual rotation. However, we expected participants receiving post-trial KR to adapt to a lesser extent (e.g. Shabbott & Sainburg, 2010) and at a slower rate than participants receiving concurrent cursor feedback, due to potential difficulties processing delayed error signals (Hinder et al., 2010). Additionally, only the concurrent visual feedback (CF) group was expected to show strong after-effects following adaptation. If the absence of concurrent feedback encouraged implementation of explicit control processes (and the absence of implicit processes), both post-trial KR groups would be expected to have longer RTs and more variable aiming performance during the adaptation phase and a reduced magnitude of after-effects (if any) compared to a the group receiving concurrent feedback during the adaptation phase. Because the rotation was introduced gradually in Experiment 1 and because this would be a strong(er) test of the effects of post-trial KR on adaptation, we introduced the rotation gradually in Experiment 2.

If we found similar effects to those of Hinder et al. (2008, 2010) this would suggest that post-trial feedback operates differently from concurrent feedback when a learner has no previous visuomotor experience and that “real-time error perception” is needed for updating of internal models. It would also provide evidence that the post-trial explicit error signal operates differently when an individual has recently acquired a novel visuomotor map for aiming in a novel visuomotor environment (i.e., Experiment 1 results). If we were unable to replicate these differences between online and offline feedback, we would then not be able to make any special claims about the operation of explicitly-driven error detection processes following practice. Rather, the presence of after-effects following only post-trial feedback would suggest that real-time error detection is not a prerequisite for implicit adaptation and that implicit adaptation occurs somewhat irrespective of the nature of the error signal.

3.2 Methods

3.2.1 Ethics statement.

Same as Experiment 1.

3.2.2 Participants

Thirty, self-reported right-hand dominant participants who were naïve to the task were randomly allocated to 3 groups: a Concurrent Feedback group (CF; n = 10; *M* Age = 21.1 yrs; Females = 7) which received concurrent continuous feedback of their cursor trajectory during each aiming movement, and two separate post-trial terminal feedback groups that received either post-trial terminal feedback of their cursor trajectory (KR_cursor; n = 10; *M* Age = 21.4, Females = 7) or post-trial terminal feedback as a numeric error score (KR_#; n = 10; *M* Age = 19.2, Females = 6). These 3 groups were further divided into 2 subgroups that had different lengths of practice during the adaptation phase (Short vs Long). The longer procedure was adopted half-way through testing because participants in the KR_# groups were unsuccessful at reducing their performance error to the same level as the cursor feedback groups with only 75 trials of exposure to the 30° CW rotation (Short Practice). An additional 100 trials of practice were therefore added. This addition allowed us to control for any potential differences in after-effects that could be explained by final aiming accuracy at the end of practice. As in Experiment 1, participants were volunteers selected from a convenience sample of UBC students.

3.2.3 Task and apparatus

Same as Experiment 1.

3.2.4 Procedure

For a summary of Experiment 2 procedures, see Table 4.

Group	Familiarization (normal)	Pre-test (normal)	3 min Break	Adapt (30°CW – gradual)	After-effects (normal)	Numerical KR Instructions & Strategy	Test (30°CW – immediate)	Rotation Awareness (Pen & Paper)
CF (n=10)	All t=20 On-line FB: Full CT No KR	All t=20 No CT No KR	Sit and rest	t=100 (Short Amt) or t=200 (Long Amt) On-line FB: Full CT	All t=20 No CT No KR	All	All t=20 No CT Off-line FB: #	All
KR_cursor (n=10)				t=100 (Short Amt) or t=200 (Long Amt) Off-line FB: Full CT				
KR_# (n=10)			# KR instruction & strategy	t=100 (Short Amt) or t=200 (Long Amt) Off-line FB: #				

Key:
All: all groups performed the condition
t: trials
FB: visual feedback
CT: cursor trajectory
KR: Knowledge of Results
#: number
Amt: Amount of practice

Table 4. Procedures for the experimental conditions in Experiment 2.

All participants first performed aiming movement to 5 targets in a normal, non-rotated environment with concurrent visual feedback of the cursor trajectory. This was conducted over 20 trials so participants could familiarize themselves with the constraints of the task. It was at this point that participants were told that their goal was to guide the green cursor through the target, moving as fast as possible while maintaining accuracy. They were also instructed that the line drawn must be as straight as possible and they were discouraged from making any corrections to their trajectory once the movement had been initiated. This familiarization phase was followed by a normal-aiming pretest to provide a baseline measure of normal aiming without any visual feedback of the cursor trajectory (see Experiment 1).

In the adaptation phase, a visuomotor rotation was introduced gradually in increments of 5° every 5 trials up to a maximum of a 30° CW rotation of the cursor feedback relative to the position of the participant's index finger. The CF group received continuous on-line cursor feedback of the rotated cursor trajectory. The post-trial feedback groups received either the trace of their last trial cursor trajectory (KR_cursor) or a numeric error score that showed the number of degrees that they missed the target (KR_# group). The post-trial feedback was provided immediately after the completion of each trial and remained on the screen for1 second. A movement trial was considered completed once participants had exceeded a radial distance of 9.5 cm from the centre of the central starting square. Participants in the KR_# group were told that negative scores indicated errors in the CCW direction relative to the target, positive scores indicated error in the CW direction, and a score of zero indicated that the participant accurately hit the target. They were not told that this feedback was erroneous (rotated by 30°). All participants were told that their goal was to achieve accurate aiming performance (a score of 0°

for the KR_# group; draw a straight line with the cursor through the target for the KR_cursor and CF groups) while moving as quickly as possible. All participants were reminded of the instructions on 5 occasions at the beginning of the gradual adaptation protocol (after every 5 aiming trials) and one more time after the completion of their 100th trial (only for participants who received 200 aiming trials during the adaptation phase).

The test of after-effects was performed in the normal environment without cursor feedback. This test was performed immediately following the end of the adaptation phase. Participants were told that they were back in a normal environment. They were asked to draw a straight line through the target by moving as fast as possible. They were also told that they would not see the cursor or receive any feedback pertaining to target accuracy.

The test for after-effects was followed by a 3 minute break where participants were given instructions about the upcoming environment. In this final test, participants were again required to aim in the "rotated" environment. Participants in all groups were asked to aim to targets in the absence of feedback and with only post-trial numeric KR alerting to their success in hitting the target. This feedback was again "rotated" such that an actual error score of 0° corresponded to a 30° CW rotation of the position of the index finger relative to the target. Participants were not told that the feedback was erroneous, but just to get the numeric score close to 0°. They were given this instruction once before the start of this condition and again after 10 aiming trials had been completed. This condition was included in order to assess/re-assess aiming performance with post-trial numeric feedback to see if what had been acquired during the adaptation phase was retained. This condition also allowed us to make between feedback group comparisons to see if later performance with only numeric post-trial KR varied with the type of feedback experienced during the previous adaptation phase.

At the end of the experiment participants completed a pen and paper assessment of their explicit awareness of the rotation experienced during the adaptation phase (same procedure as Experiment 1, see Figure 2). They were also asked questions about their awareness of the rotation imposed in the adaptation phase of the experiment.

3.2.5 Measures and analyses

The same dependent measures used in Experiment 1 were collected for this experiment. Our primary dependent variable of interest was directional constant error (in degrees) from the target measured at peak tangential velocity of the movement trajectory. Reaction time (RT) data were also collected as a measure of movement planning. Reaction time was calculated from the time of target presentation to movement onset. Movement onset was defined as the point in time when the cursor left the central home square. Variability in aiming accuracy (standard deviation of constant error in degrees) was also calculated as an indirect measure of explicit strategy use. Aiming trials where movement time (MT) exceeded 1000 ms were excluded from analyses. We were less concerned in this experiment about participants moving slowly because in 2 of the 3 groups, performance feedback was provided only once the aiming movement was completed (i.e., negating the need for online corrections). Aiming trials where reaction times exceeded 1500 ms were also excluded from analysis. These criteria changed from Experiment 1 to allow for more off-line processing time to accommodate the additional difficulty of adapting manual aiming to post-trial feedback. This resulted in a mean exclusion of 3.4% of the total trials executed by all participants (CF = 3.5 %, KR_cursor = 2.9 %, KR_# = 3.9 %), which was comparable to Experiment 1.

Mixed-factor analyses of variance (ANOVA) were conducted with feedback (CF, KR_cursor, KR_#) and amount of practice (Short, Long) as the between-subject factors.

Repeated measures were conducted on the remaining factors: phase (Pretest vs Posttest) and block (2 or 10). Partial eta squared (η_p^2) values are reported as measures of effect size. Post-hoc analyses were conducted using Tukey HSD ($p < 0.05$) and Greenhouse-Geisser corrections to *df* were applied for violations to sphericity.

3.3 Results

The performance accuracy data for Experiment 2 are summarized in Figure 7 below.

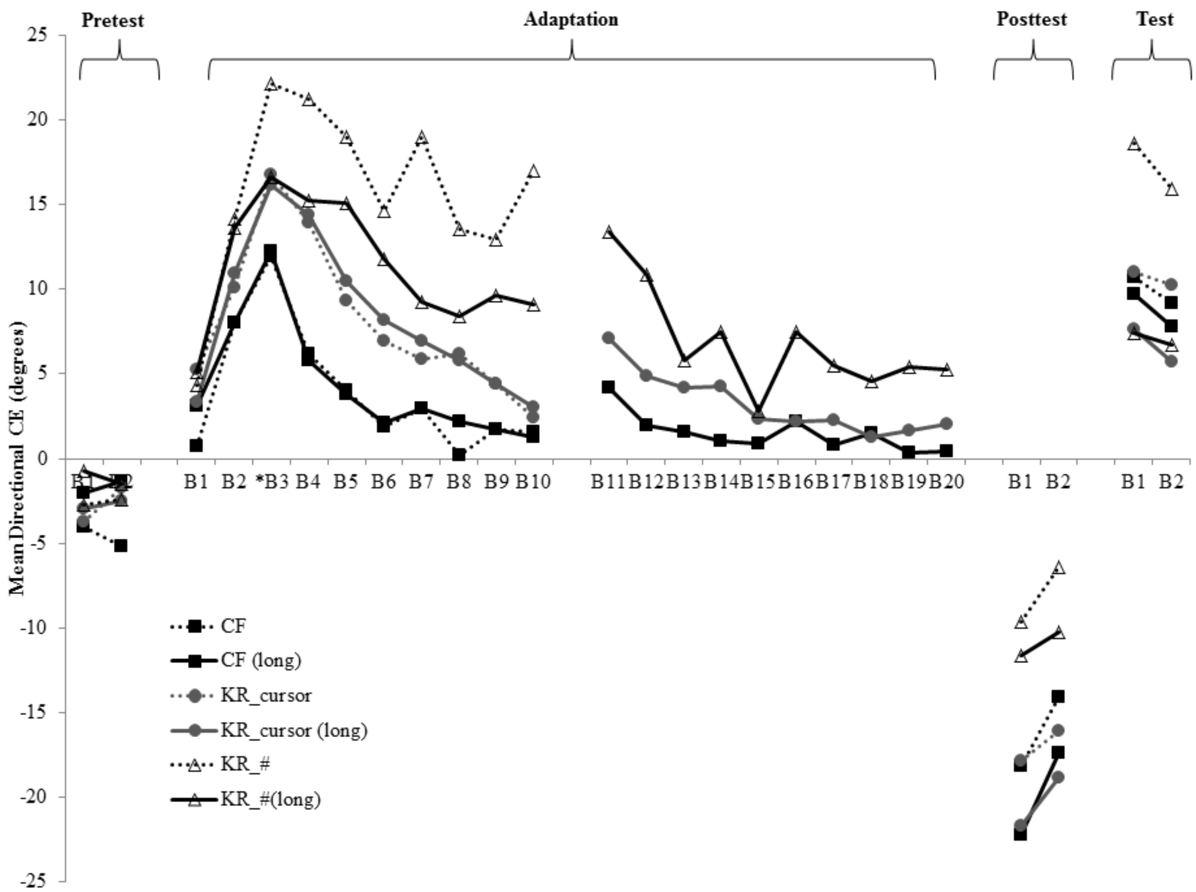

Figure 7. Mean directional CE of aiming performance reported as a function of Block (B) during the Pretest, Adaptation phase, test of after-effects (Posttest), and final test of 30° CW environment with numeric KR performance feedback. There was no rotation during the Pretest and Posttest. A negative value means that error was in the CCW direction to the intended target. The 30° CW visual rotation was introduced gradually during the first three blocks of Adaptation (rotation at 30° CW by *B3) and immediately during the Test phase.

3.3.1 Performance during adaptation

Because participants received different amounts of practice during adaptation, we conducted 2 separate, mixed factor ANOVAs. In the first analysis, we conducted a 3 Feedback X 2 practice Amount X 10 Block ANOVA (n = 10/gp) to assess early aiming performance in response to different types of performance feedback. The second analysis was a 3 Feedback X 10 Block ANOVA used to compare the last 10 blocks (n = 5/gp) of the adaptation phase for those participants who received extended practice. These procedures were used to analyze the CE, RT and VE data collected during the adaptation phase.

(i) Evidence for gradual adaptation and reduction in error with practice

As depicted in Figure 7, all groups became increasingly more errorful in the first 3 blocks in response to the incremental gradual adaptation protocol. Following the full introduction of the 30° CW rotation, participants were then able to reduce their performance error with practice. This adaptation effect was evidenced by a significant main effect of block, $F(3.33, 80.07) = 48.50$, $p < 0.001$, $\eta_p^2 = 0.67$. The 3 feedback groups performed differently during early adaptation, $F(2, 24) = 21.84$, $p < 0.001$, $\eta_p^2 = 0.65$, and these group differences varied across block, $F(6.67, 80.07) = 4.85$, $p < 0.001$, $\eta_p^2 = 0.29$. From inspection of Figure 7, we see that both the KR _cursor and KR_# groups were more errorful than the CF group at the end of the gradual adaptation protocol (Block 3). Although all groups reduced their error by the end of block 10, a post-hoc comparison of mean aiming error during block 10 of practice revealed that the aiming error of the KR_# group was significantly larger than the other 2 groups (ps < 0.05). Both the KR_cursor and CF groups did not differ at the end of block 10. The Amount of practice variable did not affect acquisition (Fs < 1) as all groups had received the same number of practice trials at this point.

Between-group comparisons were made over the last 10 blocks of the adaptation (B11-B20) to determine if any differences remained at the end of practice as a result of the different types of performance feedback. Participants continued to reduce their aiming error as evidenced by a statistically significant block effect, $F(5.11, 61.36) = 7.90$, $p < 0.001$, $\eta_p^2 = 0.40$. Although the KR_# group still appeared to be more errorful even in this second block of adaptation (see Figure 7), the feedback effect, $F(2, 12) = 3.18$, $p = 0.078$, $\eta_p^2 = 0.35$, and Feedback X Block interaction, $F(10.23, 61.36) = 1.19$, $p = 0.31$, $\eta_p^2 = 0.17$ were not statistically significant.

(ii) Longer reaction times during adaptation for the numeric KR group

Group mean reaction times during the adaptation phase are reported in Figure 8 below as averages of 10 trial blocks.

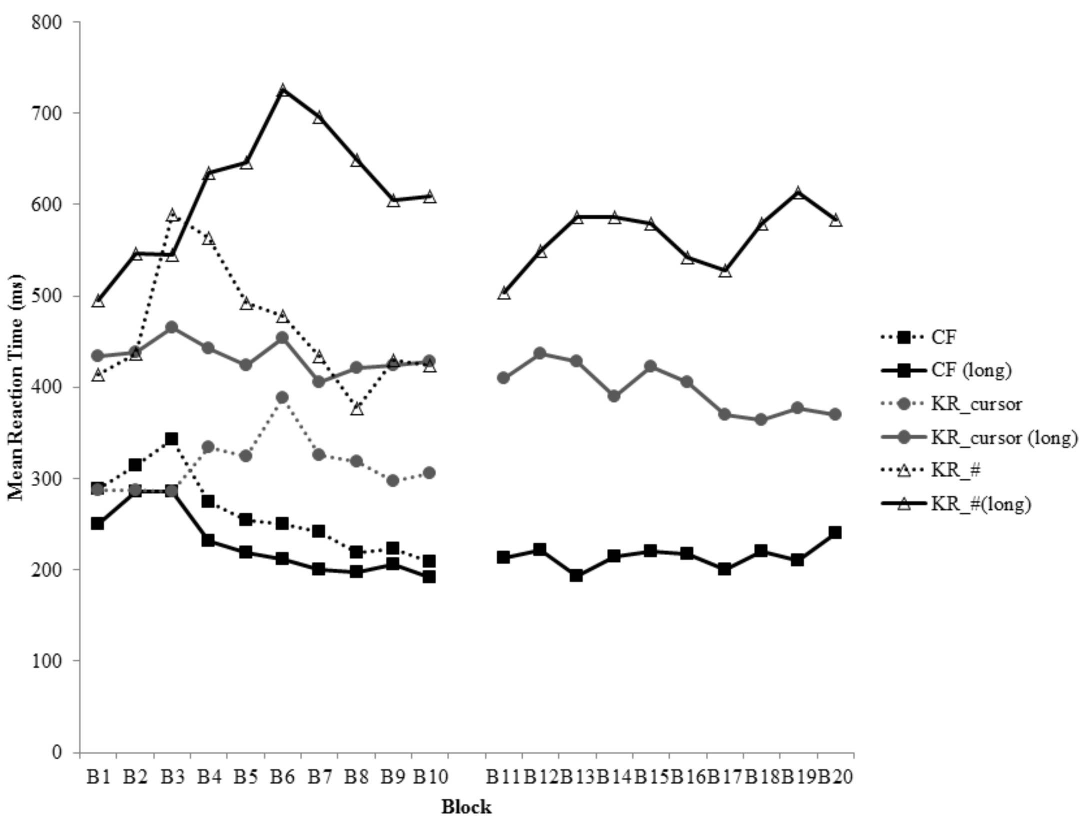

Figure 8. Mean RT reported as a function of Block (B) during the Adaptation phase.

Across the first 10 blocks of the adaptation phase there was a significant block effect, $F(4.68, 112.35) = 3.01$, $p = 0.014$, $\eta_p^2 = 0.11$. The different types of feedback provided during adaptation resulted in between-group RT differences as demonstrated by significant feedback, $F(2, 24) = 11.46$, $p < 0.001$, $\eta_p^2 = 0.49$ and Feedback X Block, $F(9.362, 112.35) = 2.25$, $p = 0.022$, $\eta_p^2 = 0.16$ effects. As can be seen in Figure 8, there were no consistent decreases in RT across practice blocks (except for the CF groups). The KR cursor groups were relatively consistent in their RTs across practice whereas the KR_# groups showed increases (short) and decreases (long) with practice. There were, however, no significant effects of practice Amount.

A separate 3 Feedback X 10 Block ANOVA was conducted on the last 10 blocks of the adaptation phase for those participants who received extended practice. Between-group RT differences were maintained in the last 10 blocks of adaptation and fluctuations across blocks were minimal. This was confirmed by a significant effect of feedback, $F(2, 12) = 11.17$, $p = 0.002$, $\eta_p^2 = 0.65$, but no block ($F < 1$) nor Feedback X Block effects, $F(6.95, 41.69) = 1.07$, $p = 0.40$, $\eta_p^2 = 0.15$. The CF group had shorter RTs than the KR_# group ($p = 0.001$), although it was not statistically different from the KR_cursor group ($p = 0.07$). The KR groups were not significantly different from each other ($p = 0.10$).

(iii) Increased variability in trial-trial error when adapting with numeric KR

The group mean within-subject error variability data is presented in Figure 9 below.

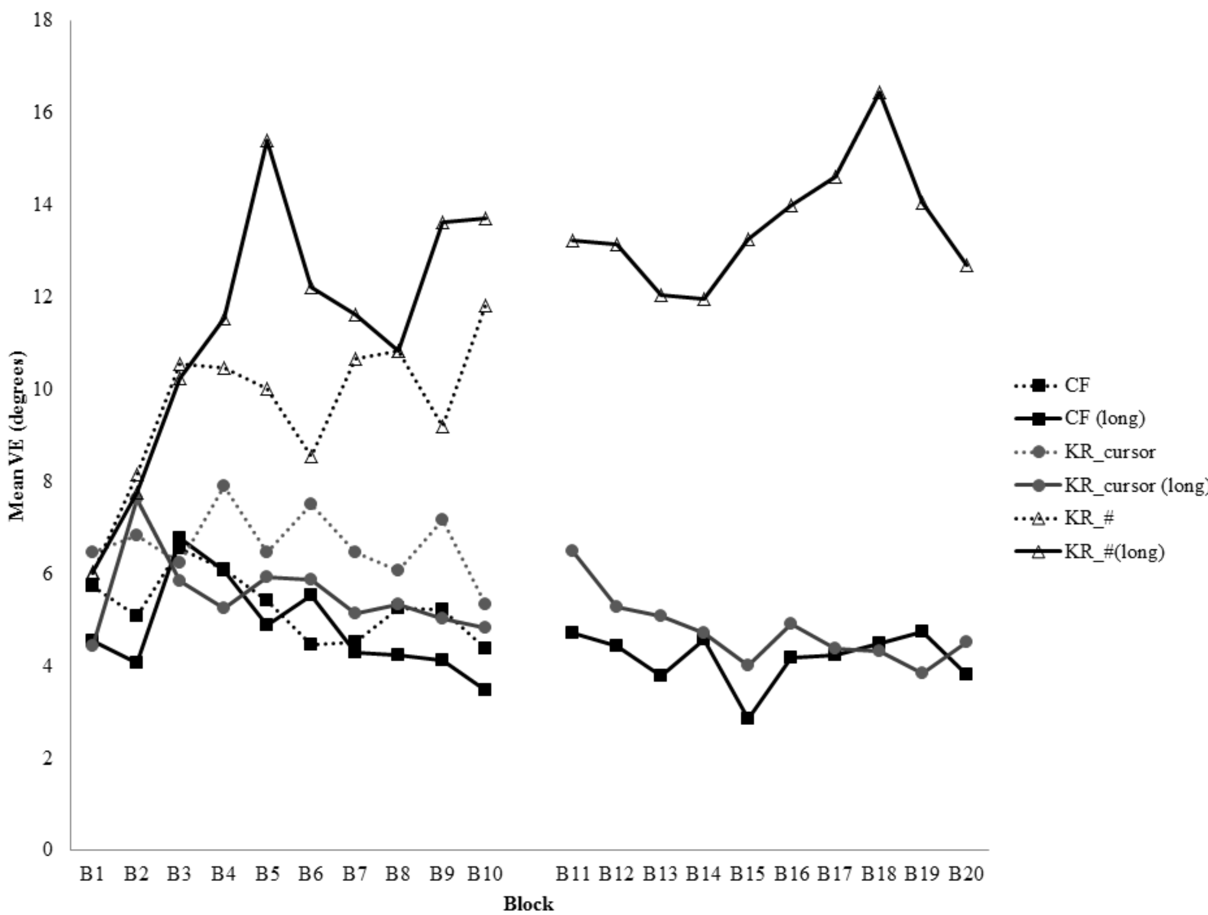

Figure 9. Mean VE of aiming performance reported as a function of Block (B) during the Adaptation phase.

From Figure 9 we see that the KR_# groups were more variable than the other feedback groups and variability of aiming accuracy increased throughout the adaptation phase for the KR_# groups, but generally decreased for the CF and KR_cursor groups. During the first 10 blocks of practice this was evidenced by significant feedback, $F(2, 24) = 66.55$, $p < 0.001$, $\eta_p^2 = 0.85$, block, $F(5.37, 128.86) = 4.18$, $p = 0.001$, $\eta_p^2 = 0.15$ and Feedback X Block effects, $F(10.74, 128.86) = 5.05$, $p < 0.001$, $\eta_p^2 = 0.30$.The mean within-subject trial-trial aiming variability of the KR_# groups was statistically greater than that of the KR_cursor and the CF groups (ps < 0.001). The CF and KR_cursor groups were not different. Although there was no effect of practice amount ($F < 1$), there was a statistically significant Feedback X Amount of practice effect, F(2,

24) = 4.29, p = 0.026, η_p^2 = 0.26. This was primarily due to the differential increase and decrease in variability for the two KR_# groups early in acquisition. The mean VE of the KR_# (long) was statistically greater than both CF groups, and greater than the KR_cursor (long) group (ps < 0.05). Practice Amount did not interact with block.

In the last 10 blocks of the adaptation phase mean trial-trial aiming variability remained relatively consistent and there were no significant effects involving block (Fs < 1). However, the differences between the feedback groups remained, F(2, 12) = 35.13, p < 0.001, η_p^2 = 0.85. The KR_# group had statistically more trial-trial aiming variability in the last 10 blocks of practice compared to both the KR_cursor and CF groups (ps < 0.001). The KR_cursor and CF group were not different.

3.3.2 Evidence for after-effects following adaptation with concurrent and post-trial cursor feedback

Aiming accuracy in the normal environment (Posttest) was consistently biased in the CCW direction compared to Pretest aiming performance before the adaptation phase (see earlier Figure 7). This was evidenced by a significant main effect of phase, F(1, 24) = 437.42, p < 0.001, η_p^2 = 0.95. There was also a significant feedback group effect, F(2, 24) = 14.38, p < 0.001, η_p^2 = 0.55 but more importantly a Feedback group X Phase interaction, F(2, 24) = 17.22, p < 0.001, η_p^2 = 0.59. The groups were not different in the pretest, but following adaptation to their respective types of feedback, the CF and KR_cursor groups had larger magnitude of after-effects (error means in Posttest) compared to the KR_# group (ps < 0.05), although they did not differ from each other. All 3 groups showed a significant increase in error from pretest to posttest (ps < 0.05). Despite there being no significant effect of practice amount, F(1, 24) = 1.44, p = 0.24, η_p^2

= 0.056, participants that received a longer practice schedule also had larger magnitude of after-effects in the posttest relative to the shorter practice groups, which was confirmed by an Amount of practice X Phase interaction, $F(1, 24) = 15.59$, $p = 0.001$, $\eta_p^2 = 0.39$ and follow up post hoc testing. There was also a significant block effect, $F(1, 24) = 31.86$, $p < 0.001$, $\eta_p^2 = 0.57$ and a Phase X Block interaction, $F(1, 24) = 18.56$, $p<0.001$, $\eta_p^2 = 0.44$ which captures the decrease in aiming error in block 2 relative to block1 during the Posttest. The block effect did not depend on the between-subjects' factors of Feedback or Amount of practice.

3.3.3 Final test of adaptation with numeric KR yielded no group differences

A 3 Feedback group X 2 Amount of practice X 2 Block ANOVA was conducted on the final Test phase to see how all groups performed with numeric KR pertaining to the 30° rotation (see far right of Figure 7). There was no significant feedback group effect, $F(2, 24) = 1.93$, $p = 0.17$, $\eta_p^2 = 0.14$. There was however a significant main effect of practice amount, $F(1, 24) = 8.48$, $p < 0.01$, $\eta_p^2 = 0.26$. Not surprisingly, participants that received more practice performed with less error in the final Test phase than those that received less practice. Although from Figure 7 it appears that errors decreased across blocks, this was not statistically significant, $F(1, 24) = 3.46$, $p = 0.075$, $\eta_p^2 = 0.13$. The Feedback group X Amount of practice interaction was not significant, $F(2, 24) = 2.02$, $p = 0.16$, $\eta_p^2 = 0.14$, nor was the 3-way interaction ($F < 1$).

3.3.4 Gradual adaptation successfully led to lack of explicit awareness about the type of error

Explicit awareness of the 30° CW visual rotation of the cursor trajectory was assessed at the end of the final Test phase. The gradual adaptation protocol was successful in preventing explicit awareness of the rotation. Only 2 out 30 participants reported being aware of error in their feedback (i.e. a rotation) and were able to correctly identify the direction of the rotation (erroneous KR) for all 5 targets (both participants in the KR_# group). See Table 5 below.

Feedback Group	Practice Amount	Dir (n)	*M* Rotation (°)	*M* Between-Target SD (°)
CF	Short	0 / 5	0.88(1.99)	5.79 (3.43)
	Long	0 / 5	0 (0)	0 (0)
KR_cursor	Short	0 / 5	5.28 (3.69)	6.09 (3.65)
	Long	0 / 5	-0 .08(4.10)	5.19 (7.11)
KR_#	Short	1 / 5	4.86 (6.93)	3.68 (5.23)
	Long	1 / 5	5.36 (6.64)	6.15 (5.66)

Table 5. Number of participants (out of 5) who consistently reported (on schematic diagrams of the target display) the correct direction (Dir) of the visual rotation of the cursor (or numeric feedback) for all 5 targets during the adaptation phase. Mean estimated angle of the rotation from the diagrams (*M* Rotation) and mean between-target standard deviations (*M* SD) are reported in degrees (°) across all 5 targets. Between-subject SDs are reported in parentheses for each measure.

A 3 Feedback group X 2 Amount of practice between-subjects' ANOVA was conducted on the estimated size of the rotation from the target diagrams. Although the KR_# groups estimated the rotation to be larger than the other groups, the feedback group effect was not significant, $F(2, 24) = 2.59$, $p = 0.096$, $\eta_p^2 = 0.18$. There was no effect of amount of practice, $F(1, 24) = 1.30$, $p = 0.27$, $\eta_p^2 = 0.05$, nor a significant interaction, $F(2, 24) = 1.11$, $p = 0.35$, $\eta_p^2 = 0.09$. Analysis of the variability of the estimates did not yield significant feedback group or practice amount effects.

Following testing, a final interview was conducted to assess verbal awareness of the rotation and perceived usefulness of the feedback. The questionnaire data are summarized in Table 6 below.

FB Group		FB = Accurate (/5)		FB = Functional (/5)	
		Adapt	Test	Adapt	Test
CF	S	4	2	3	3
	L	0	1	4	3
KR_cursor	S	4	2	5	3
	L	2	1	5	3
KR_#	S	2	2	5	5
	L	4	4	3	3

Table 6. Summary of verbal report responses from final questionnaire about the perceived mapping between the error feedback and the actual trajectory of the index finger during aiming in the Adaptation and Test phases for each feedback group (CF, KR_cursor, and KR_#) as a function of amount of practice (S-Short, L-Long). Number of participants who correctly identified that the feedback did not accurately represent their actual finger position is reported in the centre column (FB = Accurate). The number of participants who felt they were able to use the feedback to minimize aiming errors (FB = Functional) is reported in the right-hand column. All participants received numeric error feedback in the Test phase.

In general, even if participants felt like the cursor or numeric KR feedback did not map perfectly onto their actual aiming error relative to the intended target, most participants felt like they were able to use their respective forms of feedback to help minimize aiming error during the Adaptation and Test phases.

3.4 Discussion

The aim of Experiment 2 was to determine the effects of post-trial KR on adaptation to a VMA manual aiming task when participants have had no previous practice experience aiming in the presence of a visual rotation. We predicted that if post-trial KR-related effects were due to explicitly-driven processes and that after-effects (indicative of more implicitly-driven learning) were not seen in the absence of previous experience with this task, then post-trial feedback must operate differently from concurrent feedback when a learner has no previous visuomotor experience. This would suggest that real-time error-detection processes are needed for updating of internal models (Hinder et al., 2008; 2010). If, however, after-effects are seen following only post-trial feedback, then this would suggest that real-time error detection is not required for implicit adaptation processes to occur and that the results from Experiment 1 are not a function of previous experience.

Participants adapted to a 30° CW visual motor rotation with either concurrent cursor trajectory feedback or post-trial feedback. Post-trial feedback was provided as a cursor trajectory or as a numeric error score conveying target error (in degrees). Consistent with previous findings, and our predictions, all groups, were able to use their respective types of feedback to adapt to the visual rotation. We also predicted that the post-trial KR would engage explicit control processes as evidenced by longer mean RTs and more variable aiming performance during the Adaptation phase. Despite this evidence for a more explicit form of learning, we saw evidence of after-effects following adaptation in both post-trial KR groups (i.e. cursor trajectory and numeric). This finding alone suggests that, contrary to previous literature (e.g. Hinder et al., 2008; 2010; Shabbott & Sainburg, 2010), real-time error detection is not essential to bring about after-effects (via implicit control mechanisms).

3.4.1 Post-trial numeric KR encourages strategic "workspace sampling" to minimize aiming error

During the adaptation phase, we expected that all participants would be able to use their respective forms of feedback to achieve accurate performance. With enough practice aiming in the presence of erroneous or rotated feedback participants were able to minimize their aiming errors to successfully guide the cursor through the target or achieve a numeric aiming score close to zero degrees. It took more practice trials for participants who received numeric feedback about their aiming errors to minimize their error within 5° of the target. This is arguably due to the fact that interpreting a numeric value and translating it into physical movement correction is more difficult than using visual cursor trajectory feedback. Although the feedback groups were not statistically different at the end of the adaptation phase, the KR_# feedback group was still more errorful than the other 2 feedback groups. The lack of a statistically significant difference between groups is therefore likely to be a power issue because of our small sample size in the extended practice groups.

The increased difficulty of using the numeric feedback instead of cursor trajectory feedback is further illustrated by the differences in RT data between feedback groups during adaptation. Participants who adjusted aiming movements in response to numeric KR took longer to initiate their aiming movements once the visual target had been presented compared to the other groups. We suspect this is a result of the increased cognitive processing demands associated with interpreting the numeric feedback. Another, yet related interpretation of these RT data, is that post-trial numeric feedback encourages a more explicit/strategic manner of adaptation as participants require more processing time to formulate an appropriate aiming strategy. Although not statistically significant (p = 0.07), the average RT values during adaptation for the KR_cursor feedback groups were also elevated compared to the feedback group that received concurrent cursor feedback (CF). This is consistent with the findings of Shabbott and Sainburg (2010), who suggest that these RT differences are due to the timing of when error information is received. They suggest that delayed error information brings about a compensatory strategy to offset visual rotations/perturbations. The success of these compensatory strategies can be observed in the participants' ability to minimize their average aiming error with practice as well as through changes in trial-trial variable error scores. In their study, Shabbott and Sainburg (2010) observed that post-trial KR led to increased trial-trial variability with practice and improvements in error reduction were associated with these increases in trial-trial variability. Based on their results, the authors claimed that the KR group did not learn a new visuomotor map (or adapt an existing visuomotor map for manual aiming), but rather employed a strategy for reducing error with practice. In early trials, the post-trial feedback group resorted to some sort of guessing strategy. After completion of each movement the cursor feedback would tell them whether or not their guessing strategy was correct. If their strategy was incorrect, they would attempt a different strategy until they successfully acquired the target. The authors referred to this guessing strategy as "workspace sampling" and suggested it as an explanation for the increased variability in directional error and occasional correct responses. This workspace sampling strategy seems like an appropriate explanation for the aiming behaviour we saw with our KR_# group who had consistently larger trial-trial variability of aiming directional error compared to the other 2 groups. However, unlike the findings of Shabbott and Sainburg (2010), the trial-trial aiming variability of our KR_cursor group was not statistically different from the concurrent feedback group throughout practice. Therefore, although this "guessing" strategy might explain the numeric KR groups' behaviour, it does not appear to explain performance of the delayed cursor feedback group. We will give a possible rationale for why we see a difference in findings for post-trial KR across these 2 studies later in the discussion as it also may be responsible for another difference in one of our dependent measures.

3.4.2 Discussion of after-effects: KR (concurrent or post-trial) leads to implicit adaptation

As predicted, concurrent cursor feedback during manual aiming led to the largest magnitude of after-effects. Post-trial cursor trajectory feedback, however, led to comparable magnitude of after-effects. These findings are in conflict with our predictions made based upon the findings of Shabbott and Sainburg (2010) and Hinder and colleagues (2008; 2010), who only showed evidence of after-effects following aiming practice with concurrent cursor trajectory feedback. These authors had suggested that remapping requires concurrent comparisons between visual and proprioceptive inputs in this type of paradigm (i.e. a dynamic error signal). However, our findings suggest that a different conclusion is warranted.

3.4.3 An unpredicted result: numeric KR leads to after-effects

We predicted that due to the more explicit nature of the task, that we would not observe after-effects with the KR_# group. Despite this group's VE and RT data suggesting engagement and implementation of more explicit-type/strategic processes to reduce aiming error, it also displayed after-effects compared to normal pre-test aiming. However, it is important to note that the magnitude of these after-effects were still statistically smaller than the groups that received visual feedback of their cursor trajectory. It is possible that these after-effects could have been further minimized if a feedback delay was present (in our study it was provided immediately) or if feedback was provided in the test for after-effects (more detail below in section 3.4.4). What is most interesting is that despite explicit strategic adjustments, when error was present, the error signal (discrepancy between the visual feedback received and the predicted position of aiming limb) still resulted in implicit adaptation. Because the magnitude of the error signal (30° CW visual rotation) was the same for all 3 feedback groups during practice, yet the KR_# group had smaller magnitude of after-effects, it would appear that the variable workspace sampling strategy enabled participants receiving post-trial numeric feedback to minimize directional aiming errors (with extended practice) resulting in a different magnitude of implicit adaptation.

3.4.4 Why does post-trial KR result in after-effects in some studies but not others?

There are some potentially important methodological differences between our study and the studies conducted by Shabbott and Sainburg (2010) as well as Hinder and colleagues (beyond the different physical task constraints discussed previously) that may explain the different results.

(i) Feedback delays

One important methodological difference between our study and the study conducted by Hinder et al. (2010) is the timing of the feedback presentation for the post-trial KR feedback groups. In our study, the post-trial KR (both cursor trajectory and numeric) was presented immediately after the participant's finger had exceeded a radial distance of 9.5cm (distance of radius between centre of start square and centre of aiming target). In the study conducted by Hinder and colleagues (2010), post-trial KR of the cursor trajectory was presented approximately 4 seconds after movement completion (based on estimates of RT and MT). Delayed visual feedback has been shown to affect the magnitude of adaptation in humans using both prism goggles (Kitazawa, Kohno & Uka, 1995) and computer-based VMA paradigms (Honda, Hirashima & Nozaki, 2012a; Honda, Hirashima, & Nozaki, 2012b). When a 200 ms delay was artificially introduced between the participant's hand and cursor trajectory while moving in the presence of a visual rotation, learning rate (ability to reduce aiming error over time) was degraded compared to a group who adapted with no feedback delay (Honda et al, 2012a). This effect was alleviated in a 3rd group that received exposure to the feedback delay in a pre-training condition before any visual rotation was implemented. In a follow-up study, the same group of researchers examined the effect of feedback delay on the magnitude of after-effects (Honda et al., 2012b). The largest magnitude of after-effects was observed with participants who experienced no feedback delay during pre-training (i.e. veridical cursor feedback) and no feedback delay during adaptation (to a 10° CCW visual rotation). The magnitude of after-effects decreased as the feedback delay increased (100 ms, 200 ms, and 300 ms feedback delays were used). Given the findings that length of feedback delay influences the extent of visumotor adaptation, it is possible that the absence of after-effects for the post-trial KR group in the study conducted by Hinder and colleagues (2010) was due to the long delay that they used in their aiming paradigm, and that the absence of a feedback delay after reaching the target in our study may also explain why we did see after-effects in our KR groups. However, it is still surprising that a lack of delay between ending a movement and receiving numeric KR would moderate the appearance of after-effects given that the numeric KR group never got to actually see what their movement (feedback) looked like. Unfortunately, Shabbott and Sainburg (2010) did not report any information about the temporal delay between when aiming movements were terminated and when the post-trial KR was presented. All we know is that the KR group was instructed to wait in the final position of their reach until the KR was displayed.

(ii) Veridical cursor feedback during test for after-effects

Another important difference between our study and the Shabbott and Sainburg (2010) study was that in their pre-training phase and posttest for after-effects, veridical concurrent cursor feedback as well as veridical post-trial KR was provided to participants while they were reaching. This would have allowed for easier error minimization than in our posttest where we did not provide any cursor feedback to participants. Our test enabled a more robust measure of proprioceptive recalibration of the visuomotor map, which may be masked if concurrent visual feedback was provided such that movement could be entirely under visual feedback control (Henriques & Cressman, 2012; Redding & Wallace, 1996).

(iii) Contextual cues assist in internal model switching in VMA tasks

Researchers have used colour as a discriminative cue to facilitate the simultaneous retention of two different visuomotor mappings (e.g. Cunningham & Welch, 1994). Using different cursor and screen colours to represent rotated versus non-rotated environments in a visual-motor tracking task has been demonstrated to aid in switching between aiming strategies. As a result, biases in performance in the non-rotated environment (i.e. after-effects) that would be expected following exposure to the rotated environment, have been shown to be reduced with extended practice (multiple environment switches across 2 days of practice). In the studies conducted by Hinder and colleagues (2008; 2010), participants were presented with different colour screens for rotated (blue screen) versus non-rotated (black screen) environments. This change in colour when the visuomotor environment changed could have served as a cue that allowed participants to switch internal models to resist potentially weak after-effects when they switched back to the non-rotated environment. Yet, the same group of researchers using an identical apparatus to Hinder and colleagues (2008, 2010) found that colour cues alone were not effective at enabling simultaneous dual adaptation of two opposing 30° visuomotor rotations (Woolley, Tresilian, Carson & Riek, 2007).

(iv) Gradual exposure to rotation

Researchers have demonstrated that the way in which a visual rotation is introduced moderates the magnitude of after-effects following adaptation of manual aiming movements in the presence of a visual rotation (Kagerer et al., 1997; Ingram et al., 2000; Saijo & Gomi, 2010). We predicted that gradual introduction of the visual rotation would facilitate the emergence of (larger) after-effects, potentially in all groups, especially if this type of adaptation protocol influenced awareness and subsequent adaptation processes (Bernier et al., 2005; Sarlegna et al., 2007). Recall that in a previous VMA experiment using manual aiming, participants were introduced to a visual rotation gradually, and practice with both concurrent cursor feedback and post-trial cursor trajectory feedback led to after-effects (Bernier et al., 2005). Similarly, in our study, the visual rotation was introduced gradually for all feedback groups. Despite the fact that approximately 50% of participants reported that the visual feedback was not veridical with their actual hand movement, this protocol successfully prevented participants from being explicitly aware of the direction and size of a rotation for the visual targets. As a result, participants would not be able to resist the after-effects in a "normal environment" if they thought the environment had always been normal. In our current study, a visuomotor rotation was introduced gradually in increments of 5° every 5 trials up to a maximum of a 30° CW rotation of the cursor feedback relative to the position of the participant's index finger. However, when we introduced the KR in Experiment 1 (during Adapt2), the visuomotor rotation was immediately re-introduced because it had already been practiced. In this first experiment, participants were also aware that the post-trial numeric KR was erroneous.

To test whether or not the presence of the gradual adaptation protocol moderated the potential effects of awareness of the rotation on the magnitude of after-effects, we ran a 4th feedback group (n = 5) that immediately received post-trial numeric KR that was rotated 30° CW relative to the actual hand position (i.e., from trial 1 in adaptation onwards). Like the other participants that received a longer amount of practice, this group also received 200 aiming trials in the adaptation phase. The CE performance data of the KR_# group that received the gradual adaptation protocol and the KR_# group that received the immediate adaptation protocol is plotted in Figure 10 below.

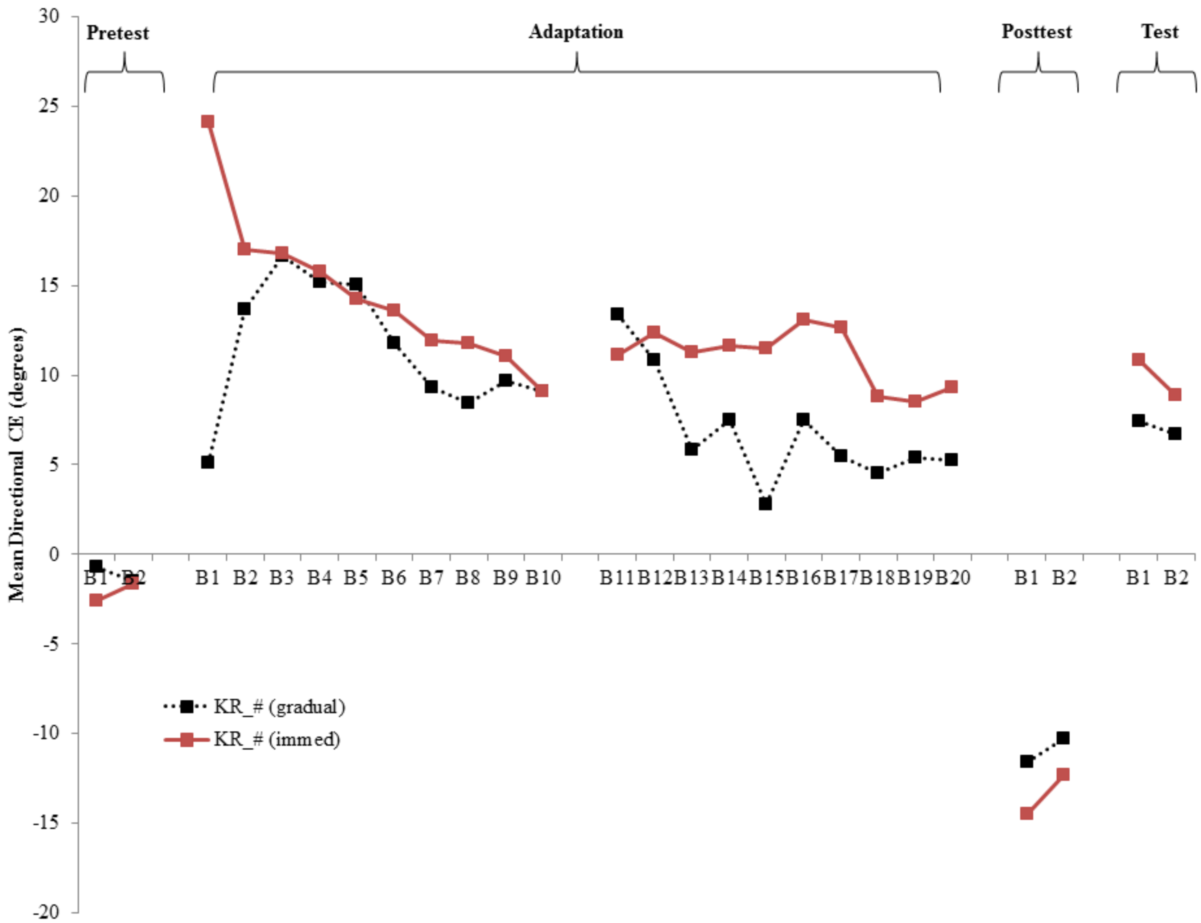

Figure 10. Mean directional CE of aiming performance reported as a function of Block (B) during the Pretest, Adaptation phase, test of after-effects (Posttest), and final test of 30° CW environment with numeric KR performance feedback. There was no rotation during the Pretest and Posttest. A negative value means that error was in the CCW direction to the intended target. The 30° CW visual rotation was introduced gradually for the KR_# (gradual) group or immediately for the KR_# (immed) group during Adaptation. The rotation was introduced immediately during the Test phase.

Statistical analyses were performed for the test of after-effects only comparing the immediate and gradual KR_# groups across the pre and posttests. There were no significant effects involving feedback group (both Fs < 1). Importantly, the effect of testing phase, $F(1, 8) = 45.37$, $p < 0.001$, $\eta_p^2 = 0.85$, showed that aiming performance was biased in the CCW direction during the posttest for both groups compared to their respective pretest performances.

Despite the immediate introduction of the visual rotation in this fourth group of participants, none of the participants in this group reported being aware of the rotation and attributed any errors in aiming performance as being self-produced as a result of the task being difficult. Although the trial-trial variability was similar across the 2 groups (gradual and immediate), the mean RT of the immediate group (M = 450 ms) during adaptation was lower than that of the gradual group (M = 590 ms). This makes it less likely that the immediate introduction of numeric feedback engaged a different, more explicit control strategy, than the gradual introduction.

(v) Error attribution

Self-attribution of errors during manual aiming in visually rotated environments has been shown to moderate adaptation effects. One group of researchers has found evidence that when learning in adapted visuomotor environments, our nervous system takes into account the perceived cause of error information (Wilke, Synofzik & Lindner, 2013). When aiming errors were perceived as being self-generated, the amount of the error signal that was attributed as internally generated correlated with the magnitude of the participants' after-effects in a perceptual probe trial (similar to our posttest where participants did not receive visual feedback of their hand or the cursor). This self-attribution may also explain why we see after-effects in our post-trial feedback groups. Some participants in the immediate and gradual KR_# groups who believed that the numeric feedback received during adaptation accurately represented their own aiming error concluded that any aiming errors were due to their personal inability to perform the task well (7 out of 15 participants reported that feedback was veridical, yet 12 out of 15 could not report correct direction and size of perturbation). This was also true of the KR_cursor group (4 out of 10 participants, yet none could report correct direction and size of perturbation). Although awareness of rotation data was not published in the studies by Shabbott and Sainburg (2010) or Hinder et al. (2010), it is possible that self-attribution of error could explain both the presence of after-effects in our study among post-trial KR groups and the absence in these other studies.

4. Summary and Conclusions

In Experiment 1, we used erroneous post-trial KR as a tool to investigate the interaction between implicitly- and explicitly-mediated adaptation for manual aiming in the presence of a 30° CW visual rotation. Implicit and explicit adaptation processes have been investigated in similar VMA paradigms and it has been suggested that they act independently to guide accurate performance (e.g. Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011). However, others have reported results that suggest that these processes are interdependent (e.g. Benson et al., 2011). In these previous experiments, an explicit strategy has been implemented immediately in the presence of a rotation, and as participants continue to practice there is evidence that the implicit process begins to dominate as both these processes attempt to drive adaptation. In our first experiment, we encouraged development of the implicit process in the absence of any competitive explicit/strategic processes by gradually introducing our visuomotor rotation. We only encouraged a more explicit type of learning in a second adaptation phase in the form of post-trial KR of endpoint aiming error. When provided with erroneous KR that increased the error signal between the actual feedback and their predicted sensory feedback, the magnitude of after-effects increased. This increase would be unexpected if implicit adaptation was impervious to explicit strategic modifications, as suggested by Mazzoni and Krakauer (2006). These findings gave us reason to suspect that explicit and implicit adaptation processes were not as independent as previously proposed.

In Experiment 2 we sought to determine if the processes encouraged by numeric KR were indeed explicitly-mediated as had been presented in the literature. To test this we compared a concurrent feedback group to two post-trial KR groups who either received numeric feedback of their aiming accuracy or a visual trace of their cursor trajectory. Participants were required to adapt aiming movements in the presence of a 30° CW cursor rotation. If the numeric KR manipulation engaged exclusively explicitly-driven adaptation processes, we would not have expected to see after-effects. This would have supported our conclusions from Experiment 1 and led to the suggestion that adaptation to KR functions differently when practicing in an environment where novel transformations relating motor commands to a desired sensory outcome have already been established. However, the results of Experiment 2 demonstrated that our method of encouraging explicit adaptation was not as robust to implicit learning as we had originally thought. After-effects were present following adaptation with post-trial KR that was gradually introduced in 5° increments. It is possible that awareness of the rotation played a role in the adaptation process, such that being unaware of an error between intended and actual outcomes resulted in implicitly-mediated adaptation processes. Yet in Experiment 1, neither awareness of the rotation nor awareness of the numeric KR being erroneous appeared to moderate the size of after-effects. Therefore it is unlikely that being unaware of a rotation is sufficient to explain the absence or presence of after-effects in these experiments.

Our data illustrate that post-trial KR, as well as concurrent cursor feedback, can bring about implicit adaptation in the form of after-effects. It is likely that some forms of post-trial KR and the method of KR delivery can encourage the implementation of more explicit forms of control such as workspace sampling strategies (evidenced by higher variable error of aiming during adaptation). From our data we see that despite the fact that adaptation to a novel visual rotation with numeric KR brought about after-effects, the magnitude of these after-effects was small in comparison to the feedback groups that received concurrent or post-trial feedback of their cursor trajectory. It is therefore reasonable to suggest that numeric KR engaged more explicit processes simply due to the fact that it required more cognitive processing to translate the number into meaningful movement corrections (evidenced by increased RTs). However this would suggest that explicit control moderated the magnitude of the after-effect thus making implicit and explicit processes competing, interdependent processes (as previously suggested by Benson et al., 2011).

We have also cited evidence that awareness of the task manipulation and subsequent attribution of the error signal can moderate the magnitude of after-effects (e.g. Wilke et al., 2013). Presumably, when participants are not aware that they are in a rotated environment, they attribute any errors in performance as being self-produced. The greater the proportion of the error signal that is considered to be self-generated, the larger the after-effect (Wilke et al., 2013). This may explain why after-effects were observed for the post-trial feedback groups. In both Experiment 1 and 2 of this thesis, post-trial feedback was provided immediately after participants reached the visual target, while other studies examining the effects of post-trial feedback had longer feedback delays (e.g. 4 s, Hinder et al., 2010). As mentioned previously, increasing the time-delay between movement completion and feedback onset has been shown to reduce the magnitude of after-effects (e.g. Honda et al. 2012a). It is possible that longer feedback delays result in decreased self-attribution of errors and hence smaller after-effects, which would explain why these other studies have not found evidence of after-effects with post-trial KR (i.e. Hinder and colleagues) and we have. The conditions that cause this self-attribution of error are not well-known. Are these effects attenuated if there is a noticeable delay in the time between movement completion and delivery of the error signal, or if the feedback provided is noticeably erroneous? These are questions that we hope to answer as we follow-up on the experiments conducted in this thesis.

We do not think that self-attribution of error and awareness of the task manipulation are the only factors that moderate the amount of implicit adaptation, because after-effects are still present, even when participants are aware the feedback they received is erroneous. Recall that in the experiment by Mazzoni and Krakauer (2006), even with an appropriate control strategy to counter the visual rotation in a manual target aiming task, participants still demonstrated after-effects. In this case, the participants knew that the error signal generated from the difference between the cursor feedback and their actual movement trajectory was the product of an externally imposed perturbation. What this tells us is that it is more likely the presence of the concurrent cursor feedback during movement that encouraged the simultaneous implicit adaptation process noted by Mazzoni and Krakauer (2006). By our definition, an explicit learning process implies strategic control which may or may not involve accurate awareness of the parameters of the adaptation manipulation. When concurrent feedback is not provided and if participants are not able to develop a successful explicit control strategy on their own (due to a lack of adequate awareness of the task rotation), it is possible that implicit, unintentional error correction processes dominate, resulting in after-effects that we saw in our post-trial feedback groups.

Additional research needs to be conducted to investigate what makes the error signal driving adaptation processes implicit or explicit. This can be achieved by measuring for after-effects after having participants adapt to a visual rotation using post-trial KR with a noticeable KR delay and by providing participants full disclosure of the experimental manipulation before having them adapt to a visual rotation with only post-trial feedback. If we find that these manipulations prevent after-effects following successful performance in the presence of the visual rotation, then we can revisit the methods adopted in Experiment 1 to see if we find the same amplification of after-effects with erroneous numeric KR feedback following an earlier, implicit learning phase.

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