

The interference effects of non-rotated versus counter-rotated trials in visuomotor adaptation

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Abstract An isometric torque-production task was used to investigate interference and retention in adaptation to multiple visuomotor environments. Subjects produced isometric flexion–extension and pronation–supination elbow torques to move a cursor to acquire targets as quickly as possible. Adaptation to a 30° counter-clockwise (CCW) rotation (task A), was followed by a period of rest (control), trials with no rotation (task B0), or trials with a 60° clockwise (CW) rotation (task B60). For all groups, retention of task A was assessed 5 h later. With initial training, all groups reduced the angular deviation of cursor paths early in the movements, indicating feedforward adaptation. For the control group, performance at commencement of the retest was significantly better than that at the beginning of the initial learning. For the B0 group, performance in the retest of task A was not dissimilar to that at the start of the initial learning, while for the B60 group retest performance in task A was markedly worse than initially observed. Our results indicate that close juxtaposition of two visuomotor environments precludes improved retest performance in the initial

environment. Data for the B60 group, specifically larger angular errors upon retest compared with initial exposures, are consistent with the presence of anterograde interference. Furthermore, full interference occurred even when the visuomotor environment encountered in the second task was not rotated (B0). This latter novel result differs from those obtained for force field learning, where interference does not occur when task B does not impose perturbing forces, i.e., when B consists of a null field (Brashers-Krug et al., *Nature* 382:252–255, 1996). The results are consistent with recent proposals suggesting different interference mechanisms for visuomotor (kinematic) compared to force field (dynamic) adaptations, and have implications for the use of washout trials when studying interference between multiple visuomotor environments.

Keywords Visuomotor rotation · Adaptation · Internal model · Interference · Consolidation

Introduction

Adaptation to novel environments occurs with repeated exposures through the formation of a mapping between the issued motor commands and the ensuing behavioural response. This mapping is known as an internal model (Kawato 1999). Experiments indicate that such adaptation is, at least partially, feedforward in nature, with feedforward motor commands compensating for changes in the external forces encountered during the task (Shadmehr and Mussa-Ivaldi 1994) or alterations of the visuomotor mapping (Krakauer et al. 1999).

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Motor learning of a new memory is thought to involve a consolidation process whereby, following exposure to a task, the corresponding memory of that task becomes progressively more stable and thus less susceptible to interference as a result of exposure to other motor tasks. A commonly used technique to examine the consolidation of internal models is the ABA paradigm. Subjects adapt to environment A (referred to as A1), before exposure to a second environment (B), followed by re-exposure to A (A2). A2 serves as a test of retention of the learning that occurred within A1. Under this experimental construct, anterograde interference is defined as interference as a result of learning task B on subsequent performance in task A2. Note that anterograde interference does not preclude consolidation of initial learning of task A1 per se, but may prohibit any consolidation from being manifested upon retest (see Krakauer and Shadmehr 2006). Anterograde interference may be manifested as aftereffects (defined as degraded retest performance of a previously learned task following an interfering task) or simply lack of retention, i.e., similar performance at retest compared with initial learning (see Miall et al. 2004; Krakauer et al. 2005). In contrast, retrograde interference occurs when task B interferes with consolidation of the learning that would otherwise occur following previous exposure to task A1. Retrograde interference is likely to result in similar performance at retest compared to initial learning, because subjects are in the same naïve (un-adapted) state. Both of these mechanisms may affect the retest performance relative to a control condition in which task B is not encountered. To discriminate between them, experimenters attempt to preclude anterograde effects by inserting washout trials, i.e., trials with no imposed dynamics or visuomotor rotation, between the A and B tasks. For example Krakauer et al. (2005) ensured subjects' performance returned to baseline levels following exposure to task B. In this manner, any anterograde interference was removed, allowing the potential consolidation of task A to be unmasked.

Brashers-Krug and colleagues (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997) reported that when the learning of two external force fields, A and B, occurred in close temporal proximity, consolidation of short-term motor memories associated with task A did not occur. The internal model of A was disrupted in learning an internal model for B. However, consolidation, i.e., resistance to retrograde interference, occurred when the temporal separation of the two fields was increased to 4 h. Furthermore, the retrograde interference effect of learning B following

A decreased monotonically as the temporal interval between exposure to A and B increased.

When considering adaptation to multiple novel visual environments, Bock et al. (2001) reported that consolidation did not occur. Interference occurred even when the time interval between presentations of the conflicting environments exceeded those intervals that permit consolidation in force-field learning. This, and similar findings in prism adaptation studies (Goedert and Willingham 2002) led to the suggestion that the interference that occurs when learning novel visual environments may be anterograde in nature. In these circumstances, B affects performance in the retest of A, rather than interfering retroactively with initial learning of A. The results obtained in subsequent visuomotor adaptation studies (e.g., Miall et al. 2004) are consistent with this proposition. Krakauer et al. (2005) reported that once anterograde effects were removed (using washout trials), retention (consolidation) of the original learning was apparent, although retrograde effects were still present to some extent.

In the current study, we used an ABA paradigm to assess consolidation and interference in a visually guided isometric torque production task, where visuomotor rotations were imposed on the visual feedback. Task B was performed immediately following initial exposure to task A. The key manipulation was the nature of the environment which the subjects encountered in task B: a counter-rotation of the visual feedback relative to that experienced in task A, or non-rotated (i.e., veridical) feedback. In this manner, we were able to test whether the nature of the interfering-task environment (rotated/non-rotated) affected the facility to consolidate and re-access motor commands appropriate for a task learned previously. This expands upon extant work that has examined whether equal and opposite rotations generate interference (e.g., Krakauer et al. 1999, 2005; Miall et al. 2004) and that which has assessed if the magnitude of a counter-rotation affects retest performance (e.g. Wigmore et al. 2002). Importantly, however, the use in the present study of a counter-rotation of a magnitude larger than that applied in task A increased the change of state between the B and A2 blocks. This facet of our study was designed to increase the likelihood that aftereffects would be manifested if anterograde interference were present. This would in turn aid in discriminating between retrograde and anterograde effects.

Consistent with recent reports, we show evidence of anterograde interference in visuomotor learning. Furthermore, our results indicate that, contrary to Brashers-Krug et al.'s (1996) result for force-field learning, for visuomotor learning, closely juxtaposed exposure

to either counter-rotated or non-rotated (null) visual environments may preclude the expression of any performance improvements when the re-test occurs in a previously learned visual environment. For visuo-motor tasks, even non-rotated (null) trials appear capable of introducing complete anterograde interference, rather than only removing the potential anterograde effects of an environment encountered previously. This finding has implications for the use of washout trials within ABA visuomotor adaptation paradigms and for the interpretation of associated results.

Methods

Subjects

Twenty-four self-reported right-handed subjects volunteered for the study. All subjects gave informed consent to the procedures, which were approved by the Medical Ethics Committee of the University of Queensland, and conformed to the Declaration of Helsinki.

Apparatus

Subjects sat 65 cm from a computer screen, positioned at eye level. The right arm was placed in a padded brace with the elbow flexed at 90° and the forearm in a neutral position. Subjects grasped an instrumented vertical cylindrical handle, with pads positioned above and below in order to minimise movement of the hand (Fig. 1, also see Shemmell et al. 2005, for further details). Forces and torques exerted on the isometric manipulandum were recorded using a 6 degree of freedom force/torque transducer (Delta ATI, Industrial Automation, USA). Force (flexion/extension) and torque (pronation/supination) were sampled at 2 kHz

Procedure

Visual feedback pronation/supination (x -axis) and flexion/extension (y -axis) torque was provided via a cursor. When subjects relaxed their arm, the cursor coincided with the start position—a yellow dot in the centre of the screen (Fig. 1).

Each trial began with a random period of 1–3 s, during which subjects were instructed to stay within the start zone. One of the eight targets, equally spaced at 45° intervals around, and at a constant distance of 5.4 cm from the start zone was then presented as a yellow dot, accompanied by an auditory tone. Subjects

were instructed to move the cursor to the target as quickly as possible by producing isometric torque in one or both of the two degrees of freedom of the elbow–forearm complex. Elbow flexion/extension torque resulted in an upward/downward cursor movement while pronation/supination torque resulted in cursor movement to the left, and right, respectively. Once the subjects had held their torque within the target zone (defined as a region of $\pm 5\%$ tolerance around the specified torque requirement) for a period of 100 ms a second tone was generated, at which point subjects relaxed, and the cursor returned to the start zone.

Each trial lasted 10 s. During trials in which the subject failed to acquire the target ($< 1\%$ of total trials) there was no second tone and the target disappeared. The trial was not repeated, and the next trial began as normal.

Subjects were randomly assigned to one of three groups (eight subjects per group), with each group undertaking three (control group) or four (test groups) blocks of trials. In each block there was a specific relationship between the direction of torque production and direction of the ensuing cursor movement. The visual feedback of cursor position was either veridical (the cursor moved in the intuitive direction) or perturbed, whereby the cursor movement was rotated with respect to the torque direction.

All groups undertook a short familiarisation (practice) block (5 trials per target, 40 trials total), during which the cursor moved in the intuitive direction, i.e., flexion torque moved the cursor up. This data was analysed but was not included in statistical procedures. All groups were subsequently exposed to a block of trials (20 trials per target, 160 trials total; block A1) in which the visual feedback of the cursor was rotated by 30° clockwise (CW, assigned negative by convention). Following A1, one group (control group) returned to normal daily activities. Two groups were subsequently exposed to another visuomotor environment (20 trials per target, 160 trials total; block B). The break between block A and B was < 1 min during which subjects stayed relaxed (as they did between each trial within the block), with their arm in the padded elbow brace (Fig. 1). The computer screen was blank during this period (the same background colour as in trials, but with no target or cursors displayed). One of these groups was exposed to trials with non-rotated visual feedback (B0 group) while the other group was exposed to a 60° counter-clockwise (CCW) rotation of the visual feedback (B60 group). Following the B block, these two groups continued with normal activities. All three groups returned to the laboratory 5 h after completion of the first block to complete a block

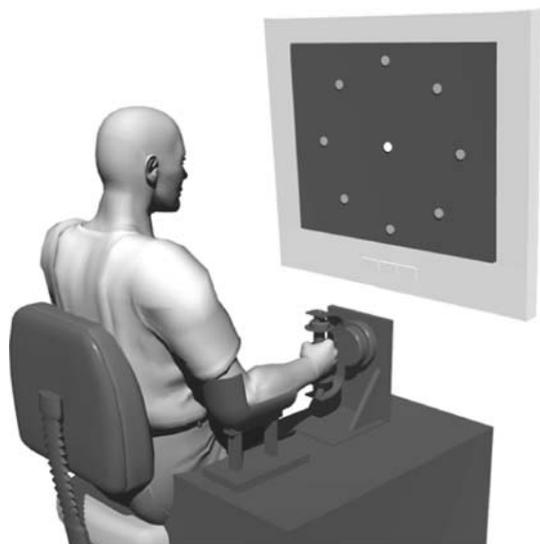


Fig. 1 Two degree of freedom isometric torque manipulandum. Subjects controlled cursor movement via isometric flexion–extension (*vertical cursor movement*) and pronation–supination (*horizontal cursor movement*) torques of the elbow–forearm complex. The start position is represented as a *white dot*. The eight visual targets, one of which was presented in each trial, are shown as *grey dots*

of trials in the original task environment, i.e., 30° CW rotation (20 trials per target, 160 trials total; block A2). The purpose of this block was to test for retention of learning in task A. Within all blocks (A1, B, A2), the trial order was pseudo-randomised such that there were 10, 16-trial cycles, each consisting of two trials to each target. Subjects received no visual or verbal cues as to the nature of the visuomotor environments within each trial block. At the commencement of each block, subjects were simply reminded to acquire each target as quickly as possible.

The resultant torque magnitude required to attain each target was identical across all subjects and targets (10–20% of subjects' maximum torque capacity). For targets representing combinations of torques in 2 degrees of freedom, the vertical (flexion/extension) and horizontal (pronation/supination) torque components were determined as the cosine of the subtended angle between the target direction and the single degree of freedom target, multiplied by the single degree of freedom torque. For all trials, the angular mapping between force/torque production and cursor displacement was unitary, i.e., x° error in the direction of torque production relative to the required torque direction (which, due to the rotation of the visual feedback, may not have been in the same direction as the visual target) resulted in an angular error of x° in visual co-ordinates.

Data reduction and analysis

Torque time series (representing cursor position), were digitally low-pass filtered at 15 Hz with a second-order, dual-pass Butterworth filter. Movement onset was determined using an algorithm based on cursor speed (Teasdale et al. 1993), with an initial threshold of 15% of the maximum tangential speed. Target acquisition, or 'movement offset', was determined as the time 100 ms prior to the second tone, i.e., the start of the first period of at least 100 ms duration in each trial during which subjects remained in the target zone. Movement time was determined as the difference between movement onset and offset.

Although movement time was used to assess overall task performance, the angular deviation of cursor paths was our primary dependent variable. Angular error, θ , was calculated as the average angle between the vector defined by the start and target positions, and the vector defined by the start position and actual cursor position, in a 10 ms window centred at 100 ms after movement onset. On the basis of the assumption that no responses based on the online visual feedback could occur prior to 100 ms, this measure assessed feedforward adaptation to the imposed rotations. Angular error was also calculated at the peak rate of isometric torque development for comparison purposes.

Enhanced feedback control, as opposed to feedforward improvements, can also lead to improved performance in a visuomotor task. This aspect of the adaptation is addressed through movement time data, which are indicative of improvements in both feedforward and feedback control. Movement time is, however, a performance measure that is dependent, for example, on the torque-cursor movement gain used in any given task (or the amplitude of the movement required in dynamic adaptation studies), and thus it does not necessarily lend itself to meaningful comparisons across visuomotor adaptation studies. In this study we focus on the improvement of feedforward control with repeated exposures to the novel task environment (rotated visuomotor mapping), which is succinctly captured by angular error. Furthermore, this measure allows meaningful comparison with previous visuomotor adaptation studies in which similar angular measures were used to monitor performance.

Data were averaged over the 16 trials in each cycle (two trials to each target). This yielded 10 values for each trial block, for each subject A power function of the form

$$y = b_1x^{b_2}$$

was fitted to the angular error and movement time data (averaged over cycles) for each trial block and each subject, using a least-squares fit criteria (Newell and Rosenbloom 1981; Miall et al. 2004). y represents the value of the dependent variable on trial x . b_1 indicates the (fitted) level of performance on the first trial while the b_2 indicates rate of learning. Such power-fitting techniques have previously been used extensively in the literature (e.g., Carson et al. 2002; Miall et al. 2004) and enable the characterization of performance throughout the learning period. They represent an alternative to approaches that focus on data obtained for specific trials or cycles of trials (e.g. Caithness et al. 2004). Only trials in which the target was successfully acquired were included in the curve fitting procedures (in <1% of trials was the target not attained). Using the values of b_1 and b_2 we obtained a predicted value for each dependent variable for the initial and final cycle of each of the experimental blocks (A1initial, A1final; Binitial, Bfinal; A2initial, A2final) for each subject. Statistical analyses were conducted on these fitted values. To confirm that the values realised from the power-fit estimations represented the data in a similar manner to other data-reduction techniques commonly used in motor adaptation studies, we calculated the average value of each dependent variable in the first and last cycle of each trial block (A1, B, A2), for each subject. Statistical analysis was also carried out using these values for comparison purposes.

Three-way (3 groups {control, B0, B60} \times 2 blocks {A1/A2} \times 2 cycles {initial/final}) ANOVA of the fitted cycle values, for both angular error and movement time data, were used to compare performance in the initial and final cycles of the original (A1) and retest (A2) in the rotated environment A. In the context of the present experimental design however, the main effect and the majority of the interaction terms generated by an omnibus ANOVA are not directly relevant. We therefore do not report the main effects and interaction terms, but focus instead on a set of pre-planned comparisons. The modified Bonferroni adjustment for multiple comparisons was used to adjust the alpha value for each comparison as appropriate, such that the effective criterion for statistical significance was maintained at the a-priori level of 0.05. Importantly, we note that because the comparisons we report were all *pre-planned*, they were not contingent upon statistically significant main or interaction terms (c.f. post-hoc tests, for which main or interaction effects *must* be significant at the a priori alpha level to allow post-hoc analyses—see Keppel 1982)

To assess retention of the performance improvements associated with initial exposure to the task

A environment, a pre-planned comparison was used to evaluate A1initial against A2initial within each subject group. We also compared performance at the commencement of block A2 between the B0 and B60 groups, to determine if altering the visuomotor environment within the B block affected initial retest performance. To aid in the interpretation of the statistical tests, effect sizes, f , were calculated (Cohen 1969). The effect size describes the degree of departure from no effect, in other words, the degree to which the phenomenon is manifested.

We conducted further analyses using the angular error data to more comprehensively assess the feed-forward adaptation to the imposed rotation. While improved performance at the onset of the retest compared with that at commencement of the original learning may be one manifestation of retention, the possibility exists that retention may also result in more rapid improvements in performance upon retest. The b_2 parameter derived from the power fitting procedure was used to compare rate of angular error reduction (i.e., performance improvement) between and within subject groups. Because this parameter is estimated using data from all trial cycles within a block it provides a robust and representative means of assessing the rate of learning. Improvements in performance between specific cycles of trials, for example, cycles 1 and 3 of each trial block, may be highly influenced by performance fluctuations within any one block, and also fail to provide an overall picture of learning within the trial block.

One way ANOVA was conducted to compare the rate of learning in the original exposure to task A (i.e., comparisons of the parameter b_2 for the A1 block) across subject groups.

Student's paired t tests were also conducted to compare the rates of learning (parameter b_2) in the initial learning (A1) and retest (A2) within each of the three subject groups. All statistics were undertaken with an a-priori alpha level of 0.05, with adjustments made for sphericity and multiple-comparisons where appropriate.

Results

Angular error

Figure 2a–c show cycle-averaged angular errors in each trial block for the three subject groups. Error bars show 95% confidence intervals. Using the power fit procedure (see Methods) values for the initial and final cycles were estimated for each trial block and are shown averaged across subjects, in Fig. 2d.

Qualitatively, angular error declined in block A1 for all subject groups, indicating adaptation to the rotated environment. Mean angular errors in the first cycle were somewhat less than the imposed rotation, suggesting that learning occurred within the first cycle i.e., subjects generalised learning across different targets within the first cycle. For groups B0 and B60, exposure to the interference block (B), resulted in paths that deviated substantially in the opposite direction to that seen in A1 initial trials. The magnitude of the errors in these blocks is consistent with subjects using the internal model that they had developed by the end of block A1, i.e., an aftereffect was apparent. As with block A1, learning within the first cycle of block B lead to a cycle average that was of somewhat lower magnitude than that seen in the very first B trial. Initial performance in the retest of A (block A2) varied markedly across groups. The control group exhibited angular errors similar to those at the end of initial training. Group B0 exhibited angular errors similar to those seen at the *start* of A1, while the angular errors observed for group B60 were greater than even those seen at the start of A1.

Figure 3 shows the change in angular error between the last cycle in the original (A1) block and the first cycle in the retest (A2) block, for each of the three groups. Although this data is also presented in Figs. 2d, 3 highlights the inter-group differences in the levels of interference. For the control group, the change in angular error is close to zero, indicating that initial performance in the retest was not dissimilar to that following the original learning. However, for the B0 and B60 groups, non-zero changes in angular error are

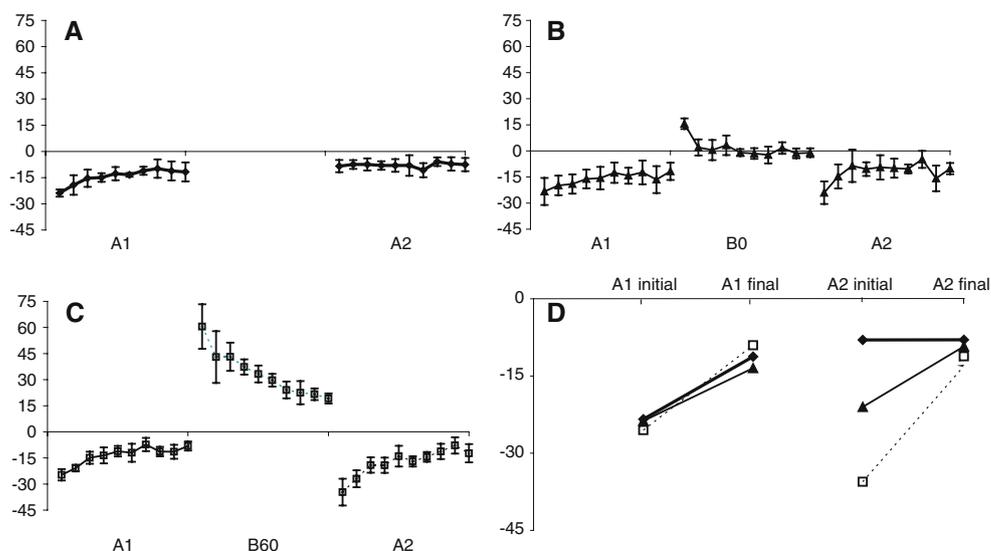
indicative of interference, i.e., errors in the first retest cycle were more strongly biased in the direction of the imposed rotation (CW assigned negative by convention) compared with the final cycle in the initial learning block.

Comparison of initial learning and retest performance

To quantify the between-group differences apparent in Figs. 2 and 3, and described above, we performed statistical analyses. These analyses realised similar outcomes using actual cycle means and power-fit estimates, indicating that the two methods are comparable. Furthermore, results for angular error calculated at the peak rate of isometric torque development mirrored those for angular error at 100 ms. In this paper, we report results for the power-fit values for angular error at 100 ms. The correlation co-efficient associated with the power fits obtained for each individual subject averaged 0.65.

Pre-planned comparisons, rather than an omnibus ANOVA, were used to compare initial performance in the learning and retest blocks (A1initial compared to A2initial) for each subject group. For the control group, initial retest performance was significantly better than that observed at the start of the initial learning, i.e., paths were more accurately directed towards targets resulting in lower angular error ($P < 0.05$, $f = 1.58$). For the B0 group, there was no appreciable difference between initial and retest performance ($P = 0.28$, $f = 0.28$). Importantly, this indicates that exposure to the non-rotated environment (B) precluded the

Fig. 2 Angular errors. **a–c** Angular error ($^{\circ}$) at 100 ms for the control, B0 and B60 groups, respectively, for the 10 cycles in each block (A1, B, A2) of trials. **d** Average fitted values (see **Methods**) for the initial and final cycles for the A1 and A2 blocks (control: *thick line, closed diamonds*; B0: *thin line, closed triangles*; B60: *dotted line, open squares*)



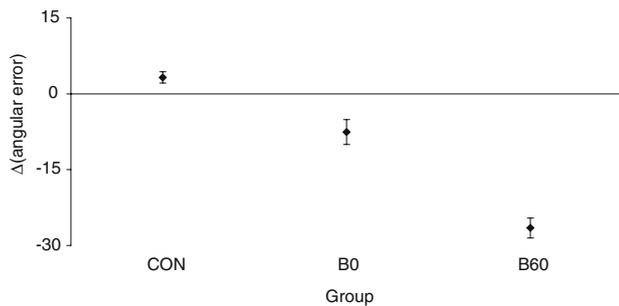


Fig. 3 Change in angular error. Change (Δ) in angular error ($^{\circ}$) between the final cycle in the original learning (A1final) and the first cycle in the retest (A2initial) for the control (CON), B0 and B60 groups. Error bars indicate 95% confidence intervals

manifestation of the performance improvements associated with the initial exposure to task A (A1). For the B60 group, retest performance was worse than that exhibited at the commencement of the original learning ($P < 0.05$, $f = 1.03$). A comparison of the initial retest performance (A2initial) between groups B0 and B60 indicated that angular error was higher in the B60 group compared to the B0 group ($P < 0.05$, $f = 1.49$) (Fig. 2d).

Comparison of learning rates

One-way ANOVA failed to reveal reliable differences in b_2 (the index of the rate of learning) across the three subject groups ($P = 0.12$; $f = 0.30$) in the first A block (A1). Thus, as expected, the original adaptation to the imposed 30° rotation occurred at rates that were not dissimilar across groups.

Student's paired t tests indicated that for the control group, the rate of reduction of angular error in the retest (A2) was significantly less than during initial learning ($P < 0.05$, $f = 0.72$). This is presumably because the skill level acquired during initial exposure to the task was retained such that further appreciable performance improvements did not occur in A2, as indicated by similar performance in all A2 cycles (note the similarity of A1final, A2initial and A2final for the control group in Fig. 2d). For the B0 and B60 groups, however, the rate of performance improvement in the retest was not dissimilar to that exhibited in the original learning period (B0: $P = 0.98$, $f = 0.01$; B60: $P = 0.62$, $f = 0.04$). Thus, for both B0 and B60 groups, it appears that the B block interfered with retention of the initial performance improvements in task A. Not only was retest performance no better than performance in the original learning (i.e., for both groups, angular errors for A2initial were not less than those angular errors in A1initial), performance improvements in the retest

occurred at rates not dissimilar to those observed in the initial learning. Any retention, in terms of ability to learn faster upon retest, should have been reflected in this measure.

Movement time

Movement time (MT) values for the initial and final cycles of each trial block were estimated for each trial block using the power fit procedure employed for angular error (see [Methods: Data reduction and analysis](#)). To enable clearer inter-group comparisons, MT was normalised to the A1initial value within each group. Figure 4 shows the normalised initial and final values averaged across subjects for the A1 and A2 blocks.

Reduction of MT within blocks may reflect improvement in feedforward control (as indicated by reductions in angular error in Fig. 2) together with improved feedback control (i.e., faster corrections to acquire the presented target). Increases in MT at the commencement of a new block are most likely reflective of inaccurate feedforward commands that require substantial feedback adjustments to allow target acquisition. As was the case for angular error (Fig. 2d), Fig. 4 indicates that all groups adapted similarly within the original exposure to task A (A1 block) with respect to reductions in MT. For the control and B0 groups, initial retest MT (A2 initial) was significantly *shorter* than that in the initial trials of the original exposure, A1 initial ($P < 0.05$; $f = 0.48$, 0.37 for the control and

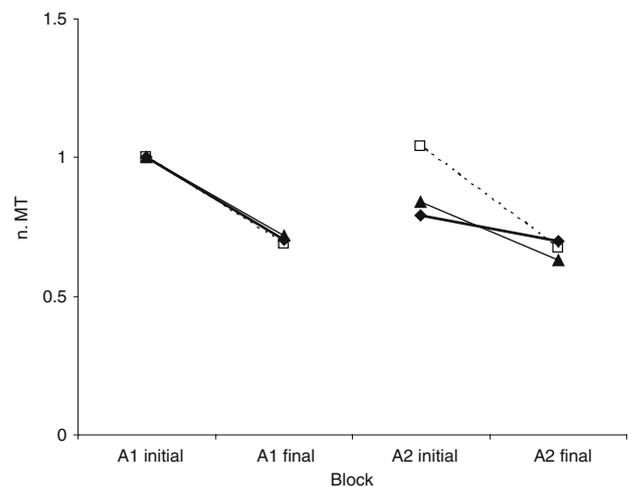


Fig. 4 Normalised movement times. Average fitted values (see [Methods](#)) for the initial and final cycles for the A1 and A2 blocks (control: thick line, closed diamonds; B0: thin line, closed triangles; B60: dotted line, open squares), normalised within each subject group to the A1 initial value.

B0 groups, respectively). In contrast, for the B60 group initial retest MT was not significantly different than in the original learning ($P = 0.35$; $f = 0.10$). Furthermore, initial retest MT was longer for the B60 group compared with the B0 group ($P < 0.05$; $f = 0.48$) indicating that the two interfering tasks (B0 and B60) had differing effects on the MT. Furthermore, as one would expect, the extent of relearning in block A2 appears to vary as a function of the extent of the interference. For the B60 group, large MT decreases were apparent within the A2 block, with smaller reductions for the B0 group. The control group exhibited minimal MT reductions across the A2 block, presumably because the adaptations underlying the performance improvements exhibited within the A1 block had been retained.

Discussion

In this study we considered whether the motor memories that were formed as a result of exposure to a novel visuomotor environment (a 30° CCW rotation) could be consolidated and re-accessed when a second task that comprised of an incongruent visuomotor environment was closely juxtaposed with the initial task. Previous studies considering visuomotor adaptation have generally investigated learning and consolidation effects when visuomotor rotations of varying direction and magnitude are learned in close succession (e.g., Krakauer et al. 1999; Miall et al. 2004). In the present study, we altered the visuomotor environment in task B, to consist of either a counter-rotation relative to that experienced in task A, or a non-rotated (intuitive) visuomotor mapping. Our results are consistent with previous reports (e.g., Krakauer et al. 1999; Wigmore et al. 2002; Miall et al. 2004), but, because we used both non-rotated and counter-rotated interference (B) tasks, we were able to expand on the existing literature and report novel findings.

The decision to use a non-rotated (B0) and 60° CCW rotation (B60) interfering task was made for several reasons. While numerous studies have considered juxtaposition of equal and opposite rotations (e.g. Krakauer et al. 1999, 2005; Miall et al. 2004), far fewer have considered an interfering task (task B) consisting of a rotation of a different magnitude to that experienced in task A (Wigmore et al. 2002). Furthermore, non-rotated trials have not generally been used as an interfering task per se; rather non-rotated trials are most often used in conjunction with a counter-rotation as ‘washout’ trials (e.g., Caithness et al. 2004; Krakauer et al. 2005). However, Krakauer et al. (2005) did

conduct a control experiment in which a number of ‘washout’ trials were employed between task A1 and task A2 in the absence of a counter-rotated interference (B) task. This study will be described later in the Discussion section.

By using a 60° CCW rotation rather than a 30° CCW rotation in task B, the change in task environment when re-exposed to task A (A2) following B was three times as large (rather than twice as large for paradigms that employ equal and opposite counter-rotations) as the change in state when subjects were first exposed to task A (A1) following initial (non-rotated) practice trials. This facet of our design may have engendered angular errors upon retest that were larger than those errors exhibited upon initial exposure (A1), i.e., aftereffects. These aftereffects enabled us to determine that the mechanism of interference for the B60 group was, at least partially, anterograde in nature.

Angular error

Changes in angular error measured prior to any online corrections in cursor trajectory clearly show improvements in feedforward performance with repeated exposures within blocks of trials (i.e., block A1, B and A2). This is consistent with the development of a more accurate feedforward internal model of that novel environment. Improved performance at the onset of task A2 compared to initial performance in task A1 was found for the control group, indicating that the subjects were able to recall, and re-issue the appropriately adapted motor commands following the 5 h break. This finding shows that learning to adapt to a rotation of the visual feedback in an isometric task occurs in a similar manner to that described previously for the adaptation of reaching movements to similar visual perturbations (e.g. Krakauer et al. 1999; Tong et al. 2002; Wigmore et al. 2002). Moreover, similar adaptations to visuomotor rotations in isometric and dynamic tasks is predicted from the results of Krakauer et al. (1999), who showed that learning of a rotated frame of reference occurred independently of the underlying system dynamics.

For the B0 group, initial A2 performance was not dissimilar to initial A1 performance, while for the B60 group, initial A2 performance was worse than initial performance in task A1 (Fig. 2). These results suggest that in this context, exposure to a second novel task immediately after exposure to the first task precludes the initial performance improvements from being manifested upon retest, *even in circumstances in which the visuomotor mapping encountered in the second task is veridical.*

For the B60 group, the finding that initial retest performance was worse than the performance exhibited at the beginning of the original learning period indicates that anterograde interference was present in the current paradigm. We cannot, however, rule out the possibility that retrograde effects were also present. Exclusively retrograde interference effects, however, would be predicted to lead to similar performance at the beginning of the initial learning period and at commencement of the retest. Thus, our results are consistent with the hypothesis that in relation to adaptation to visuomotor rotations, the interference that results from an interposed task is at least partially due to anterograde effects (Bock et al. 2001; Miall et al. 2004; Krakauer et al. 2005).

Despite the initial retest performance for the B60 group being worse than that observed at the beginning of the original learning, angular errors did not approach those which would be predicted as a result of full anterograde interference. Mean angular error in the final cycle of task B was 22.7° , indicating an adaptation of 37.3° to the imposed 60° CCW rotation. We note that the error in the final B60 trials is somewhat larger than the error following adaptation to task A, or indeed the non-rotated B task (B0). This may be due to a reduced rate of learning in the B60 block as a result of anterograde interference caused by block A (consistent with the multi-rate model proposed by Smith et al. 2006). Despite this somewhat incomplete learning of task B60, however, levels of performance in the retest of task A were lower for the B60 group than for the B0 group. Upon exposure to task A2, the expected shift between the adapted state in task B60 (37.3° CCW, i.e., $+37.3^\circ$) and the rotation then applied in A2 (30° CW, i.e., -30°) was -67.3° . The angular error was however only -36.6° in these trials. A similar, but less pronounced, trend was found for the B0 group. Following adaptation to task B, this group exhibited angular errors of 0.6° (i.e., fully re-adapted to the non-rotated task). On initial exposure to task A2 angular errors of -30.6° would have been predicted, while the manifested error in the first cycle of task A2 was -21.0° . The differences between the predicted errors and those recorded can only be partially accounted for by the learning exhibited within the 16 trials of the first cycle of the A2 task (data not displayed). The incomplete manifestations of the expected interference in our data are akin to the results reported by Miall (Miall et al. 2004) and Bock (Bock et al. 2001). Miall and colleagues (2004) reported that the proportion of the predicted aftereffect exhibited at transitions between task environments later in the experiment was lower than the proportion of the

predicted aftereffect exhibited at transitions between task environments at the start of the experiment. Our data are consistent with Miall's (Miall et al. 2004) and Bock's (Bock et al. 2001) proposal that a reduction in the level of manifested interference is due to an improved ability to adapt to the rotations (i.e., learning to learn) with repeated exposures to the any variant of task.

The effect of the interfering (B) task on movement time and angular error

Our results, indicating adaptation of feedforward motor commands such that they more accurately compensate for the imposed rotation during the course of each trial block, are not incompatible with the possibility that improvements in feedback control also occurred. Indeed, we also considered changes in MT within and between trial blocks for the three subject groups. MT may reflect the effectiveness of feedforward and/or feedback control in each task environment.

A comparison of Fig. 2d (angular error) and Fig. 4 (MT) indicates that task B had a effect on retest performance when this was characterised by angular error (measured 100 ms after movement onset) that was different to its effect on retest performance when this was characterised by movement time. While angular error reflects the accuracy of only the feedforward commands, movement times can be affected by the accuracy of both feedforward and feedback control. Indeed in this task, in which subjects produced a ballistic torque to move the cursor towards the target before subsequently modifying the torque in order to acquire the target, MT is particularly sensitive to variations in the feedback mediated terminal phase.

For the control group, initial retest angular error (A2 initial) was lower than that in the initial trials of the original exposures (A1 initial). There was also an associated decrease in MT. For the B0 group, angular errors in the A1 initial and A2 initial trials were not different. However, MT was shorter upon retest. The B60 group manifested substantial aftereffects, expressed as angular errors in the retest trials that were greater than those exhibited upon initial exposure. In spite of this, MT was not significantly different between A2 initial and A1 initial trials. Thus larger deviations in cursor path were corrected more effectively, allowing target acquisition to occur with similar movement times.

These results suggest that the interfering task had a pronounced effect on feedforward performance in the

task. This is consistent with the view that subjects modified the feedforward internal model, or visuomotor mapping, to allow accurate performance in each visuomotor environment. However, feedback control appeared to improve across all blocks of trials, independent of the rotation encountered. Subjects were able to correct a given error more efficiently with additional exposures to any rotation. This rotation-independent improvement in feedback control is to be expected, since for a given cursor error relative to a specific target, the same corrective motor command, i.e. isometric torque (relative to the initial command) is required to acquire the target under all visuomotor mappings or rotations.

Interference within visuomotor and force-field (dynamic) adaptation paradigms

In their seminal work, Brashers-Krug et al. (1996) trained subjects to make reaches in a viscous curl field, producing a clockwise (CW) force field (task A1), before they were exposed to a viscous counter-clockwise (CCW) force field (task B). The retest in the CW field occurred 24 h later (task A2). For short time intervals (≤ 1 h) between A1 and B there was no retention manifested upon retest. For longer time intervals (> 4 h) retention occurred, indicating that task B imposed retrograde interference on the prior learning of task A (i.e., at longer time intervals memories associated with task A were no longer susceptible to retrograde interference). For one subject group, task B consisted not of CCW force-field trials, but of trials with no external forces (null field), presented immediately after task A1. In this case, retention did occur, indicating that for dynamic force-field adaptation, the presence of retrograde interference was dependent on the conflicting nature (i.e., CW and CCW fields) of the two task environments, i.e., the null field did not impose retrograde interference. In contrast to the force-field learning results of Brashers-Krug et al. (1996), our results indicate that for adaptation to novel visuomotor environments, exposure to a non-rotated environment can induce interference effects: performance in the retest of task A was markedly worse for the group exposed to the non-rotated trials following initial learning compared with the control subjects who were not exposed to any conflicting task following learning. This novel result suggests that there may be differences in the way in which multiple visuomotor or dynamic environments interfere, and correspondingly that there may be differences in the way in which internal representations of these environments are consolidated.

The use of non-rotated trials as an interfering task

Very few studies have considered how non-rotated, i.e., trials with veridical feedback may interfere with a previously encountered visuomotor task. Krakauer et al. (2005) employed an ABA paradigm in which task A and B consisted of equal and opposite rotations (30° CW and 30° CCW). The results of the first experiment of their study, which did not include any ‘washout’ trials, indicated an anterograde effect- no consolidation was exhibited even when A and B were separated by 24 h. A second experiment utilised a similar ABA paradigm but in this instance ‘wash-out’ trials (trials with no rotation) were inserted immediately prior to task B, and immediately prior to the retest of task A. These washout trials were used to preclude anterograde effects of A on learning of task B as well as similar effects of B on the retest of A (Krakauer et al. 2005). In this manner, the authors address a slightly different issue from that to which we attend in our present work. We specifically designed our experiment to investigate whether non-rotated trials would themselves result in interference effects. Thus, our work provides novel results that complement the extant studies e.g., Krakauer et al. (1999, 2005) Miall et al. (2004) and Bock et al. (2001).

It is notable however that a control group in Krakauer et al.’s (2005) experiment (their group 5) were exposed to 30° CCW trials, followed by a retest in the 30° CCW rotation 48 h later (i.e., they were not exposed to the counter-rotation, task B, between the original exposure to and retest of task A). Immediately prior to the retest, ‘washout’ trials were administered to “remove anterograde effects”. The pattern of trials that this group experienced was therefore somewhat similar to the B0 group in our study. For group 5 in Krakauer’s study, initial performances in the original exposure and upon retest were not different, although the rate of performance improvements in the retest was faster. In contrast, their control group 1, who were tested in the 30° CCW rotation followed by retest 48 h later (*with no washout trials*), exhibited lower initial errors and faster learning upon retest (i.e., retention or facilitation). Thus, as Krakauer et al. (2005) note in their paper, the (non-rotated) washout trials performed by group 5 must, *to some extent*, have interfered with the facilitation that would otherwise have been manifested, i.e., as exhibited by their group 1. The results from our B0 group indicate that non-rotated trials are capable of imposing *full* interference on a previously learned task (no reduction of initial errors and no improvement in the rate of learning was found upon retest). There are, however, a number of differences

between the studies that may explain the fact that Krakauer et al. reported more rapid performance improvements upon retest in their group 5 (partial retention upon retest), while we found complete interference. Krakauer et al. (2005) used one-third as many 'washout' (non-rotated) trials compared with the number of trials in the A blocks, which may have affected the efficacy of the washout. Full interference i.e., no retention of performance and no change in the rate of learning, may require a number of washout trials that is equivalent to that undertaken in the original learning and retest blocks. It is also worth noting that Krakauer et al. (2005) gave subjects a 48 h break between task A and the administration of the 'washout' trials, after which the retest of A was conducted without further delay. The intervals between the exposures to the various environments were therefore different to those in our study. This could also account for the vagaries between the two sets of results.

The interference that we have shown for the B0 group is consistent with a recent multi-rate learning model proposed by Smith et al. (2006). This model suggests that learning consists of fast and slow adaptive systems and that adaptation is the net effect of the two systems at any specific point during the adaptation process. Smith and co-workers modelled a learning-unlearning-relearning paradigm. Relearning occurred at a faster rate than the initial learning. However, slow system had not fully de-adapted from the initial learning within the unlearning trials because there were fewer unlearning trials than original learning trials. Thus, the slow system was still in an adapted state when re-exposed to the original perturbation. Consequently, relearning was biased by the fast system compared with the original learning, resulting in a faster overall relearning. (as manifested by group 5 in Krakauer et al. 2005) The B0 block of our study (equivalent to the unlearning block in Smith et al.'s model) consisted of as many trials as had been encountered in the A1 block. This would have allowed both the fast and slow systems of the model to return to naïve (un-adapted) states. In this instance, the model predicts, as we report in this study, that learning and relearning occur at the same rate.

Summary

In summary, the interference effects observed in this isometric visuomotor adaptation task are consistent with the proposition that the interference effects that occur when two conflicting visuomotor environments are juxtaposed are at least partially anterograde in nature (Bock et al. 2001; Miall et al. 2004; Krakauer

et al. 2005). While Brashers-Krug et al. (1996) found that a non-perturbed (or null) environment does not give rise to retrograde interference when adapting to novel force fields, we have shown that non-rotated trials can impose complete interference in (isometric) visuomotor learning paradigms. This finding may have important implications when washout trials are used within ABA visuomotor adaptation paradigms. Because the non-rotated trials themselves appear to give rise to interference, caution needs to be exercised when assessing whether any manifested interference is a result of the interfering B task. It may in fact be a consequence of the washout trials themselves.

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