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RESEARCH ARTICLE

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Adaptation to rotated visual feedback: a re-examination of motor interference

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Abstract We have tested human visuo-motor adaptation in rotated-feedback tasks in which subjects first learn to move a cursor to visual targets with a rotational perturbation between joystick and cursor, and are then challenged with the opposing rotation. We then retest the subjects in the original adaptation task, to measure retention of a short-term memory of its earlier learning. Others have used similar tasks and report retrograde interference between one task and the short-term motor memory of the preceding task, such that later performance is impaired. However, we show that in the short-term conditions tested here, these effects can be considered as anterograde interference effects between the two tasks and we find no evidence of retrograde interference.

Keywords Motor control · Motor learning · Motor consolidation · Short-term memory

Introduction

There have been a number of studies of sensorimotor adaptation in recent years that have explored the effects of motor consolidation during and after transient adaptation to perturbed visual feedback or to forces applied to the hand. These reports have concluded that the close juxtaposition of two conflicting adaptation tasks can lead to anterograde and retrograde interference between the two tasks, and these results have been described in the context of interference or consolidation of short term motor memories (Brashers-Krug et al. 1995, 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997; Krakauer et al. 1999; Bock et al. 2001; Tong et al. 2002; Goedert and Willingham 2002; Wigmore et al. 2002). There is still some debate about the extent that exposure to one task, task B, can interfere with or enhance consolidation of a previously experienced but discordant condition, task A. However, we believe that in the reports published to date, there are still conceptual aspects of these reports that require further study.

First, in all those studies that have reported the condition, the effect of moving from the initial adaptation task A (which we refer to as task A_1) to task B is typically a large drop in performance (Brashers-Krug et al. 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997; Bock et al. 2001; Goedert and Willingham 2002; Wigmore et al. 2002). This can be due to anterograde interference or after-effect. The subjects are partially adapted to task A and so the switch from A_1 to B is greater than the switch from the null condition to A_1. In contrast, the level of performance measured on return to task A (session A_2) from task B is typically of the same magnitude as when the naïve subjects were initially challenged with task A_1 (Brashers-Krug et al. 1995, 1996; Krakauer et al. 1999; Tong et al. 2002; Goedert and Willingham 2002; Wigmore et al. 2002). In other words, these studies report negative transfer (anterograde interference) from task A_1 to B but do not show anterograde interference from B back to A_2.

Second, the suggestion that interference between the two tasks is due to destruction of a short-term motor memory (Brashers-Krug et al. 1995; Krakauer et al. 1999; Ghez et al. 1999; Tong et al. 2002) seems at odds with the known benefits of interleaved practise of related tasks (Shea and Kohl 1990; Cunningham and Welch 1994; Hall and Magill 1995; Roller et al. 2001). For interleaved practise to be a useful training regime, each task must leave its own trace in memory, so that both can be eventually consolidated. The differences may depend at what stage generalization of similar tasks shifts to interference between dissimilar tasks.

Finally, many of these experiments on motor consolidation use a "centre-out" design in which the subject is required to start from the centre of a circular array of targets and reach to each target on instruction. Perhaps guided by the clock-like appearance of the array, Krakauer et al. (1999), Ghez et al. (1999) and Tong et al. (2002)

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used target sequences that moved in order around the array; thus the sequence of targets is highly predictable and familiar. In contrast, Shadmehr and colleagues (Brashers-Krug et al. 1995, 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997) used a randomised order of targets in their experiments, but here the subjects adapted to a rotational force field. However, our preliminary data suggested that the target sequence might influence the magnitude of interference, and a second aim of this paper was to study this in more detail.

Our results suggest that retrograde interference is minimal in this task, and that the effects can be instead considered in terms of anterograde interference of short term motor memories, combined with generalization or learning-to-learn. Target sequence order does affect learning, but has little overall affect on interference between sessions.

Materials and methods

Task

Subjects held a small lightweight joystick in their right hand, which rested on a padded arm support, while sitting in front of a computer monitor at head height. The position of the joystick was displayed on a VGA computer monitor as a green cursor, 16×16 pixels (or approx. 0.75 degree measured at the eye). A white target circle (16 pixels diameter) was initially displayed at the screen centre surrounded by a yellow circle of radius 200 pixels or 20 degrees. The white target then alternated between the central position and one of eight equally spaced positions just inside this yellow circle (150 pixels from the centre) at a rate of one step every 750 ms (Fig. 1). The subjects were instructed to move the joystick so as to shift the cursor from the central start position to the displayed target and back to the centre in a rapid, discrete, movement. They were instructed not to correct pointing errors during each trial, but to try and rapidly move the cursor in the right direction. The adaptation challenge to the subjects was a clockwise or counterclockwise rotation of the cursor with respect to the joystick.

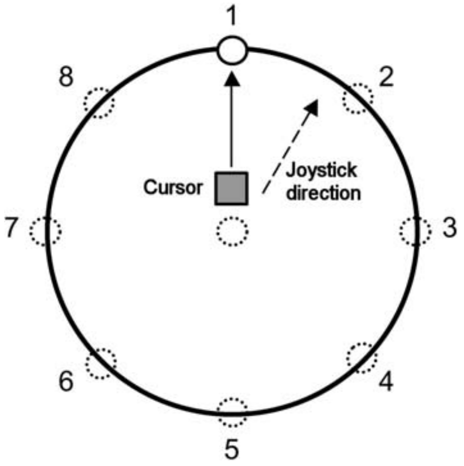

Fig. 1 Schematic diagram of the display. The joystick-controlled cursor is moved from the central position to each target and back again; at any moment only the central target or one peripheral target was displayed (target 1 is shown here, with 30 CCW rotation of the cursor from the joystick). Target numbers were not displayed on screen

The screen background gave partial cues about the conditions. In all experiments, the null condition (with no visual perturbation) had a light grey screen, whereas in all test conditions (with a visual perturbation), the screen colour was blue. Each block of trials started with the target at the top (12 o'clock position) and 17 targets were presented once every 1.5 s. For the final 3 s of the 27 s block, the word "REST" was superimposed on the screen, and subjects variably completed the 17th movement before the next block, which would then start without delay. Only the first 16 trials were analysed in each block.

Protocol

Each subject performed the following basic sequence of blocks, each block of 16 trials. The exact conditions used for each subject group are summarised in Table 1. Note that the group performing Experiment 3 varied from this sequence, by repeating phase 3 and its associated rest period twice.

Twelve practice blocks with normal cursor motion (data not shown)

- Phase 1: Null task: 12 baseline blocks with normal cursor immediately followed by
- Phase 2: Task A_1: 12 adaptation blocks with rotation of the cursor motion
- A 15-min pause, during which the subject remained in the laboratory, but either chatted or read a book
- Phase 3: Task B: 12 interference blocks with the opposing rotation of the cursor motion
- A second 15-min pause, during which the subject remained in the laboratory, but either chatted or read a book
- Phase 4: Task A_2: 12 post-interference blocks with the original rotation used in the adaptation phase, immediately followed by
- Phase 5: Null task: 12 baseline blocks with the normal cursor feedback
- An overnight pause, of between 14 and 26 h duration, during which the subjects were occupied with normal activities
- Phase 6: Task A_3: 12 consolidation blocks with the original rotation and a further
- Phase 7: Null task: 12 baseline blocks (data not shown)

Experiment 1A

Ten right-handed subjects took part (age 19–30 years, staff or students at the University of Oxford, who were naïve to the task). Five subjects (*SEQ1A*) performed the centre-out task to eight clockwise ordered sequential targets (1, 2, 3,...8), the cycle repeating twice in each block of 16 trials, in all phases of the experiment. The other five (*RND1A*) performed the task to a randomised sequence of targets, in which the order of successive blocks of eight targets was random. The only constraint on the randomisation was that all the eight targets were chosen once in each block of eight. For both groups the adaptation phases (Task A_1 and A_2) used 80-degree counterclockwise rotation of the cursor. Both groups rested for a total of 35 min between Task A_1 and A_2 (Table 1); they were tested to examine any basic difference in consolidation performance due to the target sequence.

Experiment 1B

An additional ten right-handed subjects (age 19–46) repeated the same RND and SEQ tasks as above, but were also challenged with an interruption phase, Task B, in which the opposing rotation of the cursor was used (Table 1). Five subjects (*SEQ1B*) performed the same task to sequential targets as in *SEQ1A*. The other five (*RND1B*) performed the task to a randomised sequence of targets, as in *RND1A*. For both groups Task A used 80-degree counter-

Table 1 The testing protocol used for each experiment. Tasks A and B refer to angular rotation of the cursor, by 80 or 30 degrees as specified. In each case Task B is an opposite rotation to Task A (clockwise vs. counterclockwise or vice versa). The Null task is with normal cursor feedback. Groups RND, SEQ, LRN were exposed to random, sequential CW or a repeated non-sequential target sequence, respectively

Experiment			1A	1B	2	3	4
Within-experiment subject groups (i.e. target sequence)			RND SEQ	RND SEQ	RND SEQ LRN	RND	RND
Phase	Start block	End block	Task condition (shift in degrees)				
Practice	−24	−13		Null	Null	Null	Null
1	−12	0		Null	Null	Null	Null
2	1	12	A_1 80	A_1 80	A_1 30	A_1 30	A_1 30
			All groups: 15 min gap				
3	13	24		B 80	B 30	B_1 30	B 30
			All groups: 15 min gap				
4	25	36	A_2 80	A_2 80	A_2 30	B_2 30	A_2 30
						15 min gap	
5	37	48	Null	Null	Null	A_2 30	
					Overnight gap		
6	49	60			A_3 30	Null	

clockwise rotation of the cursor, while the interruption phase used clockwise rotation by 80 degrees (Table 1); these groups therefore tested whether the interference of consolidation depended on the target sequence order.

Experiment 2

This was essentially similar to Experiment 1B, but we reduced the visuo-motor rotation of the cursor to 30 rather than 80 degrees, and included an extra subject group and additional test phases. The protocol used is shown in Table 1. Eighteen right-handed subjects (age 19–22, students at the University of Oxford who were naïve to the task and to the purpose of the study) took part after giving informed consent. Fourteen were male, four female. They were assigned to three groups of six, Group *SEQ2* performed the task to clockwise ordered sequential targets (1, 2, 3, ..., 8) as in Experiment 1B; group *LRN2* performed the task to a repeated sequence of target positions (positions 1, 4, 6, 2, 5, 7, 3, 8); group *RND2* performed to a randomised sequence of targets, as in *RND1B*. Half of each group were challenged with clockwise rotation of the cursor in Task A and counterclockwise in Task B; and vice versa for the remaining subjects.

Experiment 3

Eight subjects (age 18–47, 3 male) performed a variation on *RND2* condition of Experiment 2, after giving informed consent. Three of these had been tested in Experiment 2 more than 12 months previously. The first three phases were identical. However, in the post-interruption blocks, phase 4, these subjects were tested with the same direction of rotation as in the interruption phase. In other words they repeated the interruption condition after their second pause of 15 min (Task B_2 identical to Task B_1). As before, half the group were challenged with clockwise rotation of the cursor in Task A and counterclockwise in Task B; and vice versa for the remaining subjects. This group are labelled *RND3.*

Experiment 4

Six further subjects (age 19–23) performed a second variation on *RND2* condition of Experiment 2, again with informed consent. All phases 1–4 were identical to those used in Experiment 2 except that changing the screen colour in the interruption phase, phase 3, to dark green, provided a contextual cue. Subjects were verbally instructed that this condition was different from what they had become used to. The post-interruption blocks, phase 4, was the same as in the pre-interruption phase 2 with the same screen colour. In other words they were given contextual information that the interruption condition was novel, and of the return to the previous pre-interruption state. As before, half the group were challenged with clockwise rotation of the cursor in Task A and counterclockwise in Task B; and vice versa for the remaining subjects. This group are labelled *CNTX4.*

Analysis

The horizontal and vertical position of the joystick was continuously recorded at a rate of 50 Hz via a 16 bit AD converter (CED 1401). The radial distance of the cursor from the centre target was calculated in Matlab after filtering with a zero-phase fourth order Butterworth low pass filter at 10 Hz, and used to automatically detect the occurrence of the first 16 movements in each block. The angular deviation of the joystick measured at the moment of maximal outward velocity (typically about 150–200 ms into the movement) was then calculated with respect to the central starting target. All automatic movement selections by the Matlab script were checked by the operator, and a maximum of three movements per session (typically about 1.5%) were discarded, for example if no clear single velocity peak was seen for a given trial when a subject might fail to respond to a target. Mean directional errors across the 16 trials per block were calculated for each subject, and used in subsequent statistical analyses. In some cases, the mean block errors from the first or last pair of trial blocks from a given phase are compared, to assess the absolute levels of performance. Repeated measures ANOVAs were performed using SPSS version 10, with Greenhouse-Geisser sphericity-corrected values reported when appropriate; threshold for statistical significance was set at $p<0.05$.

To quantify learning rates, double exponential curves were first calculated for the group mean learning curves and gave very close fits (r-squared >0.98), but frequently the fit to individual subject learning curves used extreme parameter values for the first exponential (i.e. a single curve would have been appropriate). We therefore measured adaptation in each subject by fitting a single power curve to the data from each session ($y=\beta1{*}{\times}\hat{}\beta2$; the r-squared of all individual fits was better than 0.55), and used the two coefficients of these curves, β1 and β2, for group statistical analyses.

Results

Experiment 1: effect of target sequence

Figure 2 shows learning curves for the two groups when first challenged with the 80 degree CCW cursor rotation, and on returning to the same task after a pause of 35 min. Group *RND1A* followed randomly ordered targets while *SEQ1A* followed a clockwise order (Fig. 1). Trial-trial performance in these groups was quite variable, and we therefore show plots of absolute directional errors. The two groups show similar performance across all phases of the task; a 3×2×12 phase-group-block repeated measures ANOVA showed no significant main effect of group, nor any significant interaction between group and phase. There were no significant group differences or group interaction effects in the baseline phase.

Figure 3 shows the learning curves for the next two subject groups before, during and after interruption of the initial 80 degree CCW task with the 80 degree CW task. As above, there were no significant group differences in the baseline phase. However, the group tested with random ordered targets (*RND1B*) show significantly less disrupted performance during the interruption phase 3 than the group with sequential order targets (*SEQ1B*). Hence a 2×4×12 group-phase-block ANOVA showed a significant interaction between group and block ($F_{(11,88)}=2.69$, $p=0.005$) and between group, phase and block, ($F_{(33,264)}=1.69$, $p=0.013$). Directly comparing phase 3 (Task B) in a 2×12 group-block ANOVA, there was a significant group-block interaction ($F_{(11,88)}=2.18$, $p=0.022$). In both groups, there was a trend towards negative transfer from Task A_1 to Task B, as the initial errors in the first two blocks of Task B were higher than the initial two blocks of Task A_1. Comparing Task A_1 and Task A_2 (phase 2 vs. 4) there was again evidence of differential performance between the two groups (a significant interaction between group and phase; 2×2×12 group-phase-block ANOVA, $F_{(1,8)}=5.88$, $p=0.042$) and between group, phase and block ($F_{(11,88)}=1.99$, $p=0.039$).

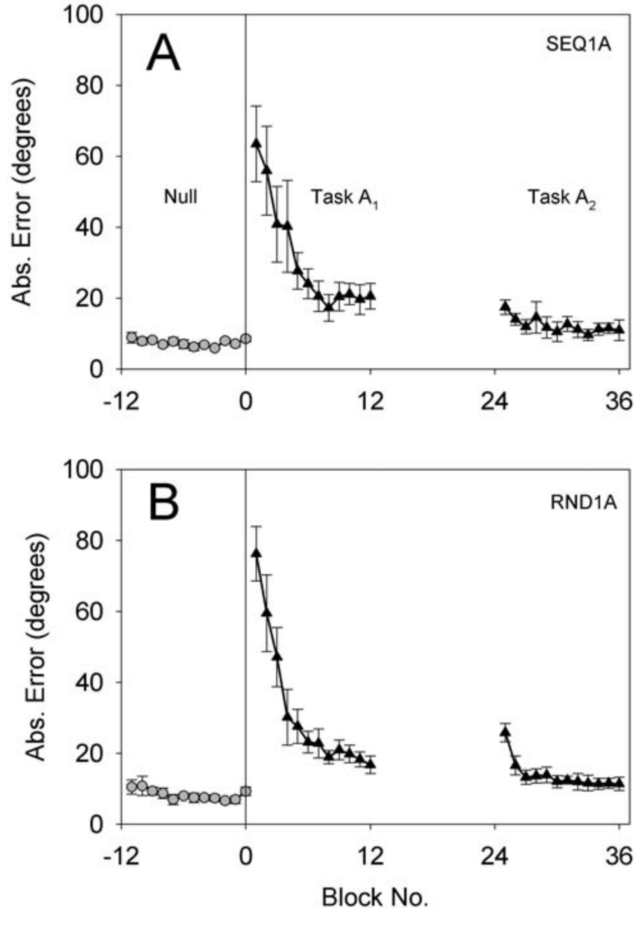

Fig. 2 Experiment 1A: Performance curves for two groups tested with sequential clockwise targets **(A)** and randomly ordered targets **(B)**. *Each datum* is the group mean (n=5, ±1 SD) of absolute directional errors across a block of 16 trials. Subjects first performed a baseline phase (*grey circles*) before being challenged with an 80 degree CCW rotation of the cursor (Task A_1, *black triangles,* blocks 1–12). After a 35-min rest, they repeated the same 80 degree condition (Task A_2, blocks 25–26; the gap here is to make the horizontal axis equivalent in Figs. 1, 2, 3, 4, 5)

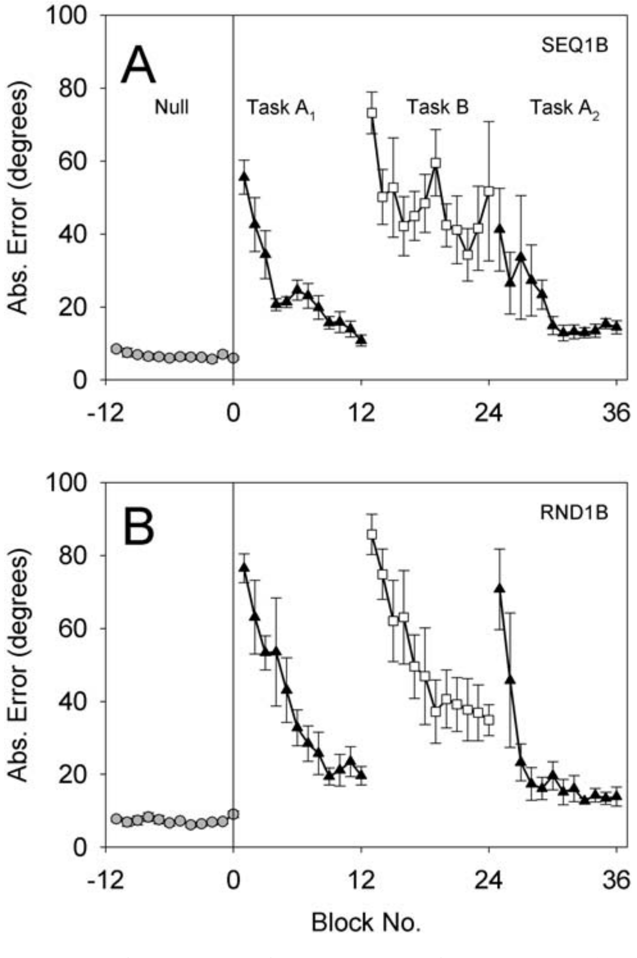

Fig. 3 Experiment 1B: Performance curves for two groups (n=5) tested with sequential clockwise targets **(A)** and randomly ordered targets **(B)**. The format is identical to Fig. 2; these groups were challenged with the interference task (Task B, CW 80 degrees, *white squares*) in blocks 13–24. Subjects had a 15-min rest between Task A_1, and Task B (i.e, between blocks 12 and 13), and between blocks 24 and 25 (Task B to Task A_2)

Summary

These initial experiments suggest that basic level of performance in adaptation to a rotated cursor is not affected by target sequence order, but that the interference effects are different in the two conditions. However, the perturbation used was large (80 degree) leading to high variability, and possibly invoking an explicit adaptive strategy (Abeele and Bock 2001b). Furthermore, total shift in cursor feedback from Task A to Task B was 160 degrees (2×80) and this may be treated as a different challenge, solved perhaps as an inversion of 180 degrees (Abeele and Bock 2001b).

Experiment 2: effect of target sequence and interference

Because of the difficulties posed by the large rotational shifts of 80 degrees used in Experiment 1, we repeated this experiment with smaller perturbation angles of ±30 degrees. Other authors (Ghez et al. 1999; Tong et al. 2002) also use this rotation magnitude. All subjects now performed this modified task adequately (note the reduced SE error bars in Fig. 4 compared to Fig. 3).

Interference effects: phase differences

Learning curves for the adaptation phases 2–5 are shown in Fig. 4. All three groups clearly show declining error curves in each phase. Each group showed larger errors at the start of Task B (the interruption phase 3) than at the start of Task A_1 or A_2 (phases 2 and 4, pre- and post-interruption adaptation). Comparing the directional errors from phases 2, 3 and 4 across the three groups, we found a significant difference across the phases in a 3×3×12 phase-group-block ANOVA ($F_{(2,30)}=15.02$, $p=0.001$). In this and subsequent analyses, the negative errors in phases 3 and 5 were inverted, to allow statistical comparison of magnitude with phases 2, 4 and 6. There was also a phase-by-block interaction ($F_{(22,330)}=3.59$, $p=0.001$) suggesting differential adaptation rates in the three phases. Directly comparing phase 2 and 3 (pre-interruption Task A_1 and interruption Task B) confirmed both points: a significant effect of phase (2×3×12 phase-group-block $F_{(1,15)}=17.29$, $p=0.009$), and a phase-block interaction ($F_{(11,165)}=7.92$, $p=0.0001$). There was a highly significant difference in β1 between Task A_1 and Task B (2×3 phase-group ANOVA, $F_{(1,15)}=22.15$, $p=0.005$) and between Task B and Task A_2 ($F_{(1,15)}=10.57$, $p=0.013$), with a non-significant difference between Task A_1 and Task A_2. There was no significant difference in the β2 parameter in either comparison. Hence there were significantly greater errors in Task B due to interference between Task A_1 and B.

Comparing directional errors for the final two blocks from phases 2, 3 and 4 (3×3×2 phase-group-block ANOVA) demonstrated no main factors of block, but a significant effect of phase ($F_{(1,6)}=7.83$, p=0.009). Performance at the end of the inference phase 3 was less good than in phases 2 or 4. Performance measured over the final two blocks of phase 5, after re-exposure to unperturbed null conditions, did not significantly differ from the final two blocks of the baseline, phase 1. All three groups had returned to stable and equal performance in the unperturbed condition.

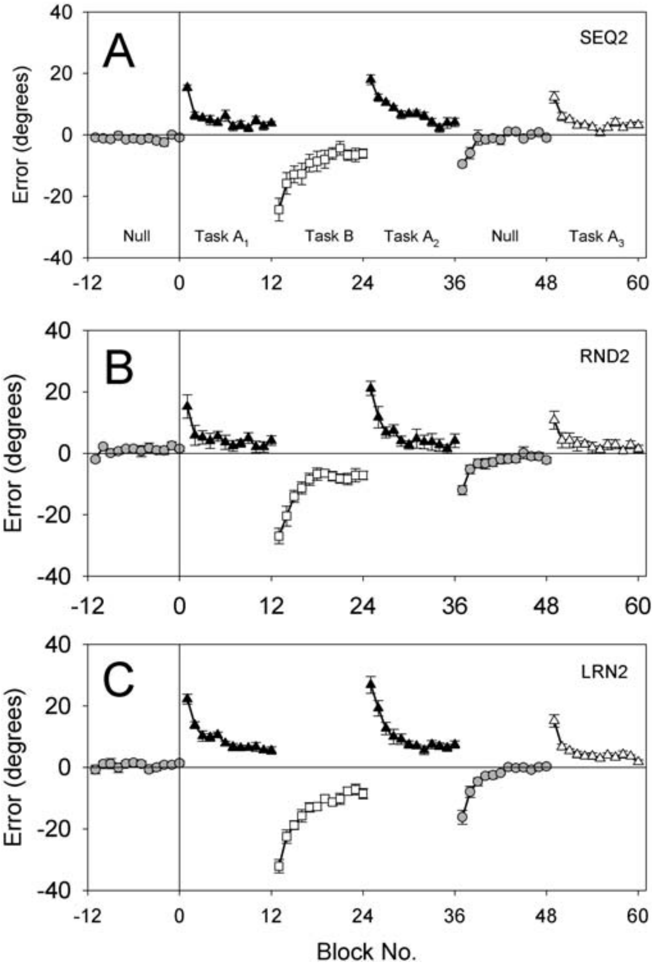

Fig. 4A–C Experiment 2: Performance curves for the three groups (*n*=6) tested in Experiment 2. In this and subsequent figures, relative directional errors are shown, averaged across blocks of 16 trials, and then averaged across subjects. In each group, half the subjects experienced clockwise rotation in Task A, and half counterclockwise rotations. The data have been inverted as appropriate before averaging. Subjects were first challenged with a 30-degree cursor rotation (*black triangles,* blocks 1–12), the opposing rotation after a 15-min rest (*white squares,* block 13–24), returned to the original rotation after another 15-min rest (Task A_2, *black triangles,* blocks 25–36), then readapted to the null condition (*grey circles,* blocks 37–48). The next day, they repeated the original 30-degree condition (Task A_3, *white triangles,* blocks 49–60). The target sequence for the LRN2 group was repetitive but non-sequential

On the following day, the three groups then repeated their original perturbed conditions (Task A_3, phase 6, white triangles, Fig. 4). All groups showed evidence of overnight consolidation with low initial errors (β1 coefficients from Task A_3 significantly lower than in Task A_1, 3×2 group-phase ANOVA, $F_{(1,15)}=18.76$, $p=0.007$) followed by a decline to baseline levels of performance. Hence in a 3×2×12 group-phase-block ANOVA, there were significant effects of phase on errors ($F_{(1,5)}$=13.86, p=0.014). However, the β2 coefficients from Task A_1 and Task A_3 were not significantly different, suggesting no group difference in re-adaptation rate.

Effect of target sequence: group differences

Directional errors in phase 1 (the baseline) did not statistically differ between the three groups or across the 12 blocks of trials in that phase (3×12 group-block ANOVA, no significant main effect of group, block or group-block interaction). Hence the baseline performance was stable and comparable between groups.

Comparing errors in the adaptation phases (2–5) in a 3×4×12 group-phase-block ANOVA, there was significant main effect of the group ($F_{(2,15)}$=4.22, p=0.047), confirmed by comparing the power curve parameters β1, showing significant group differences (3×4 group-phase ANOVA, $F_{(2,15)}$=6.12, p=0.018). There was also a significant interaction between group and block on error, whether tested across all four phases 2–5 ($F_{(22,165)}$=2.30, p=0.0001), or across only phases 2–4 ($F_{(22,110)}$=1.98, p=0.011), suggesting that the adaptation process (which leads to a difference in errors across the 12 blocks within each experimental phase) differed between the three groups. The differences between the learning rate parameter β2 were not significant, nor were there significant group-phase-block interactions. The errors in the final two blocks of phases 2–4 showed no significant group differences. Performance measured over the final two blocks of phase 5 did not differ between groups (2×3×2 phase-group-block ANOVA), showing that all groups returned to equal performance in the null condition.

Summary

Experiment 2 confirmed interference between sessions, with errors significantly higher in Task B than in Task A_1. Errors were equivalent in Task A_2 and Task A_1, suggesting either that there was no significant interference from Task B to Task A_2, or that there was no significant retention of Task A. These two suggestions will be examined in the "Discussion". Experiment 2 also showed that the sequential order of targets had a significant effect on performance with the higher mean errors for the *LRN2* group than the *RND2* group, and lowest mean errors for the *SEQ2* group, despite the three groups starting from and returning to an equal baseline. These differences were reflected in the β1 power curve parameters. However, the rate of learning (measured either by the β2 parameters or by the performance reached in the last blocks of the adaptation phases, or by appropriate group-phase-block interactions) did not show group differences.

Experiment 3: retention of interference task

Experiments 1 and 2 demonstrate that the switch from Task A_1 to B was significantly harder than the return switch from B to A_2. In fact, there was apparently little difference in switching from Task B to A_2, compared to switching from the naïve state to Task A_1. Other authors have assumed that adaptation to Task A_2 is indeed reached from a null state, the memory of Task A_1 having been catastrophically destroyed by Task B. However, if adaptation to Task B had been achieved, one would expect a detrimental effect on Task A_2. One explanation may be that switching from Task A_1 and Task B not only interferes with retention of Task A_1, but may also impair retention of Task B. Alternatively, the exposure to Task B may have been insufficient to allow full adaptation to this condition, before return to Task A_2. Experiment 3 tested these alternatives.

As expected, the adaptation curves for phases 1–3 of this experiment (*RND3,* Fig. 5) are essentially identical to those observed in Experiment 2, as Tasks A_1 and B were identical (Table 1). However, in phase 4, when group *RND3* was tested with the same perturbation as used in the interruption phase (Task B_2), all subjects clearly demonstrated consolidation of that condition. Subjects' performance in the first two blocks of phase 4 is significantly better than in the first two blocks of phase 3 (2×2 phase-block ANOVA, $F_{(1,7)}$=99.4, p<0.0001); hence the power curve β1 parameter was significantly higher in phase 3 than 4 (Student's t=8.56, p<0.0001); the learning rate parameter β2 was not significantly different. Thus adaptation in Task B_2 started from a lower error level but progressed at the same rate as in Task B_1. Finally, the level of performance at the end of Task B_1 was equivalent to that at the end of Task B_2 and A_1 (no significant phase effect, 3×2 phase-block ANOVA, $F_{(2,14)}$=1.696). As in previous experiments, the performance on return to Task $A_2$was not significantly different from that in Task A_1; the difference in performance from Task A_1 to $B_1$was, however, outside significance.

Summary

This experiment demonstrates that the interruption Task B is sufficient not only to interfere with Task A_1, as shown by Experiment 1 and 2, but also leads to significant retention of the interruption condition. It also suggests that the majority of adaptation to Task B was reached within the first phase, and no significant further adaptation took place in the repeat of this condition.

Experiment 4: effect of contextual cues

One reason the subjects generally perform worse in Task B than in Tasks A_1 or A_2 could be because of uncertainty about their current context—the different adaptation conditions in this experiment and in those by other

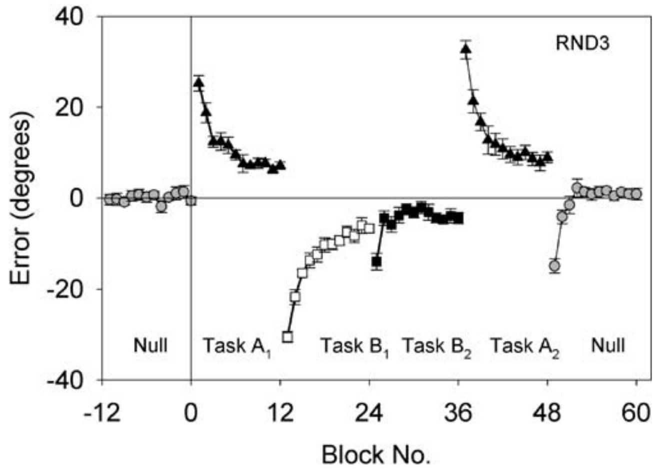

Fig. 5 Experiment 3: Performance curves for a group (n=8) tested with a repetition of the interference task. This group was challenged with the 30-degree cursor rotation (Task A_1), then the interference task after a 15-min rest (Task B_1, opposite rotation, *white squares,* blocks 13–24). After a second 15-min rest they repeated the opposite rotation (Task B_2, *black squares,* blocks 25–26), and then after another 15 min, returned to the original rotation, as in Experiment 2

scientists were implicitly presented. Hence the subject may be initially unaware on entering Task B that the situation has changed. Furthermore, on return to Task A_2 they may be unaware that the current condition is the one to which they have been previously exposed. So one can conceptually separate the process of context identification from that of motor adaptation, and both may affect performance. This was tested in Experiment 4 by providing contextual cues for Task B.

The adaptation curves for this experiment (Fig. 6) are almost identical to those of Fig. 4b. There was no significant difference between the error levels in Task A_1 and Task A_2 (2×12 phase-block ANOVA) nor between the β1 or β2 parameters for these curves (Student's *t*-tests). Comparing errors between this subject group and those in groups *RND2* and *RND3* across the baseline, Task A_1 and Task B in a 3×3x12 group-phase-block ANOVA we found no significant main effect of group, nor a group-phase interaction. Phases 4 onwards are not comparable between these groups. The level of performance at the end of phase 3 (Task B) was again equivalent to that at the end of Task A_1 (no significant effect of phase, 2×2 phase-block ANOVA).

Summary

The added information (verbal instruction and visual colour cues) about the context of each phase of the experiment had insignificant effects on performance. We can reject the hypothesis that context identification was an important aspect of performance.

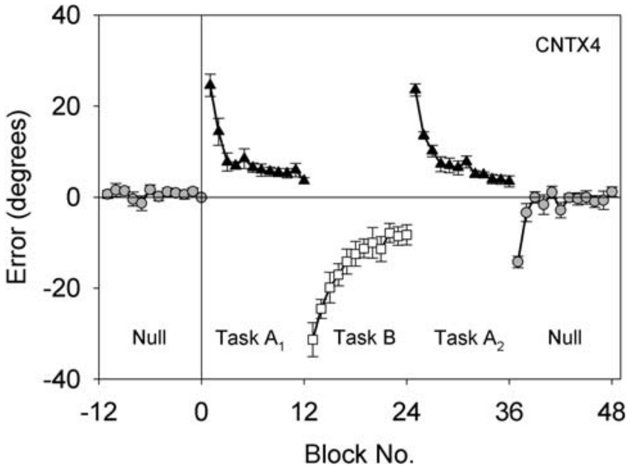

Fig. 6 Experiment 4: Performance curves for a group (n=6) tested with contextual cues. The format is similar to that of Fig. 4B. This group was cued verbally and by screen colour of the three task conditions (null, 30-degree rotation and opposing rotation). Subjects had a 15-min rest between blocks 12 and 13, and between blocks 24 and 25

Discussion

There are three main results from these experiments testing consolidation of visuo-motor adaptation. First, there is a differential change in performance when switching from one adaptation task (Task A_1) to the opposing task (Task B), compared with the change seen when switching back from Task B to the original (Task A_2). We argue below that this is not consistent with retrograde interference between Task B and A_1. Instead this is evidence that a motor memory of Task A_1 is maintained, despite exposure to Task B, and influences subsequent performance in Task A_2. Second, contextual visual and verbal cues provided to instruct the subjects of which task condition they are in have negligible effects on adaptation and performance, affecting neither level of interference nor rate of learning. Third, the sequential order of the targets used has significant effects on performance, and on the change in performance when switching between visuo-motor adaptation conditions, but does not in fact cause selective effects on the level of interference or learning rates.

Our initial experiments (1A and 1B, Figs. 2, 3) suggested there was a specific effect of the target order on motor learning interference, as the *RND1B* group showed lesser interference during Task B than the *SEQ1B* group, and faster return to good performance in Task A_2. However, the subjects reported confusion in these tasks, and the total shift in cursor rotation between the Task A and B was probably too large. Abeele and Bock (2001b) have shown that rotations up to 80 degrees are processed differently from those greater than 80 degrees: large angular shifts may even be achieved by an inversion (180 degrees) followed by a smaller backward shift. Retesting the question of target order in more detail in Experiment 2, in which three subject groups were challenged with the more frequently used 30 degree rotation, did not support the result from Experiment 1.

There was still a significant effect of target sequence on overall performance, but no specific interaction between interruption of learning and sequence order. As might be expected, the group faced with a simple predictable target sequence performed at highest level, while the group faced with the random order were less accurate. Hence additional information available to the subjects about the forthcoming target location aided their performance (e.g. Rosenbaum 1980; Bock and Arnold 1992). The group following a learned but non-sequential pattern of targets performed least accurately, suggesting a cost in remembering the target order, perhaps due to a shared-attention deficit.

Turning now to the difference between performance in Tasks A_1, B and A_2, why do our subjects, and those reported by others (Brashers-Krug et al. 1995, 1996; Krakauer et al. 1999; Tong et al. 2002), show essentially equal performance in Tasks A_1 and A_2? If they adapt to Task B, the shift required to go from their adapted state in Task B to A_2 should approximately match that required to go from their adapted state in Task A_1 to B (and in each case should be approximately double the shift from the naïve state to Task A_1). Hence we should predict about equal performance in Tasks B and A_2, in both cases, worse than A_1.

This apparent absence of interference could have been because the subjects remained in the adapted state appropriate for Task A despite exposure to Task B, i.e. they had not been able to learn during Task B. However, adaptation to Task B was very clear (Figs. 3, 4, 5). It might instead be because the two adaptation tasks mutually interfered, and cancelled each other, so that neither Task A_1 nor B could be retained in memory. If so, re-testing subjects in Task A_2 would be equivalent to testing the naïve subjects in Task A_1, consistent with their approximately equal performance levels. This possibility was tested and refuted by Experiment 3, where clear retention of Task B was seen in conditions in which we had previously seen strong interference between Task B and Task A_2 (Experiment 2). It might also be because subjects had not sufficiently adapted to Task B, before returning to Task A_2. Again, this was tested in Experiment 3, which showed that performance reached at the end of Task A_1, Task B_1 or Task B_2 was not significantly different. Finally, there might be a switching or context shifting effect in which knowledge about the current context is an important part of performance. We used implicit presentation of the two opposing tasks in Experiment 1, 2, and 3, as have others (Brashers-Krug et al. 1995, 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997; Krakauer et al. 1999; Bock et al. 2001; Tong et al. 2002), so that the poor performance in Task B relative to Tasks $A_1$and A_2 might reflect lack of knowledge of the conditions. Again, we tested this in Experiment 4, providing visual and verbal cues to the changes in conditions, and refuted the possibility.

Thus we are left with the finding that performance at the start of Task A_2, on switching from Task B, is better than expected from the performance seen at the start of Task B, on switching from Task A_1. The only explanation seems to be that retention of Task A_1 has not been blocked by Task B, but is maintained and sufficient to improve performance in Task A_2. The final two phases in Experiment 2 give additional support for this. Immediately after phase 4 (Task A_2) the subjects were tested again in the null condition, and as expected readapted quite rapidly to a level of performance identical to the baseline (Fig. 4). This null phase should have interfered with the second exposure to Task A_1. Thus, consolidation of Task A_1 should have been blocked by interference from Task B, and consolidation of Task A_2 should have been blocked by interference from the null condition, phase 5. Yet on testing the following day, performance was good in Task A_3: there was clearly good retention of the memories of Task A_1 or A_2 overnight. We suggest the retrograde interference effects are small under these conditions.

Our measure of the effects of interference, namely comparison of performance in Task A_2 versus performance in Task A_1, or Task A_2 versus performance in subjects that had not experienced the interruption (as in Experiment 1) corresponds to that used by all other groups (Brashers-Krug et al. 1995, 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997; Krakauer et al. 1999; Bock et al. 2001; Tong et al. 2002). We believe in retrospect that this measure is inappropriate. The true measure should take account of the shift in sensory-motor conditions between the task being measured and the previous task. In all these experiments where an opposing visual perturbation or force field has been applied, the shift to and from the interference condition is greater than the shift from the naïve condition to the initial adaptation condition. Abeele and Bock (2001a, 2001b) have shown that adaptation to rotated feedback is incremental, so that for example, adapting to 60 degrees from 30 degrees is easier than from the zero degree null condition. Ingram et al (2000) and Kagerer et al. (1997) have also shown similar incremental adaptation.

Thus performance measures in the adaptation tasks should reflect the magnitude of the shift between successive conditions. In Fig. 7A we plot the mean errors at the start of each adaptation phase, calculated from all five subject groups from Experiments 2, 3 and 4. Note that while the magnitude of these errors is generally less than 30, these data are calculated from the average of 16 movements, and so reflect the rapid reduction of errors during the block. Plotting the mean β1 coefficient values from the curve fits, rather than the initial errors, gives almost identical results (not shown) confirming that the β1 power curve coefficients are a good measure of initial performance. Fig. 7B then plots the group mean levels of performance measured from the first block of each phase, calculated as the percentage of the imposed shift:

$$100 \times \text{intial error}(\text{feedback shift} - \text{final error})$$

where the initial error is the mean error in the first block of each task phase (as in Fig. 7A), the feedback shift is either

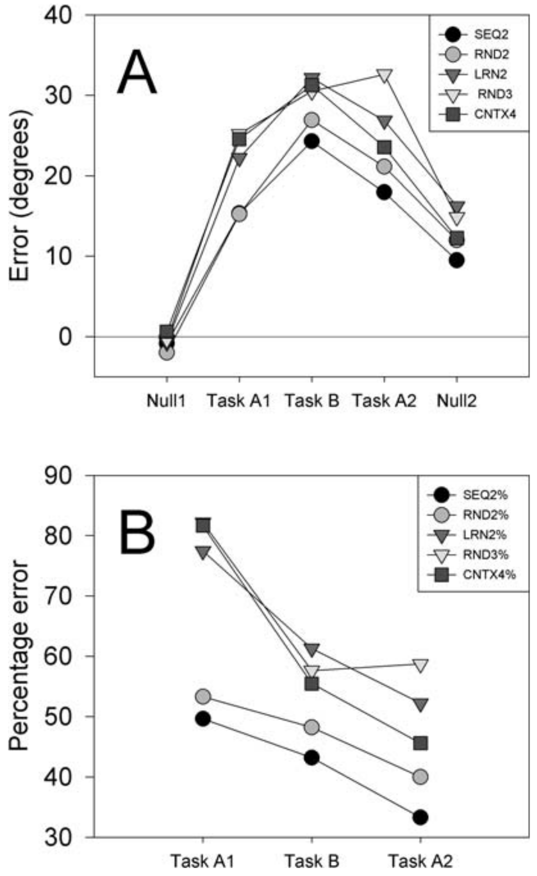

Fig. 7A, B Relative performance at the start of each phase of the experiment, for subjects tested in Experiments 2, 3 and 4. **A** The group mean errors in the initial block of trials, across the five subject groups and four phases. **B** The group mean percentage error in the first block of trials in each phase, scaled by the imposed shift in feedback angle. This measure (see main text) would result in 100% errors if subjects failed to show any compensation for the shift in feedback from one phase to another. Instead a gradual improvement in performance is seen across experimental phases

30 or 60 degrees, and the final error is the mean error in the final block of the *preceding* task phase. In this form, magnitude of the initial errors is scaled to the shift in perturbed feedback between one phase and the next, taking into account the amount at adaptation in that previous phase. In both graphs it is apparent that there is a progressive improvement in *relative* performance across Task A_1, B and A_2. If there were retrograde interference, we would predict that the errors shown in Fig. 7A or the percentage errors shown in Fig. 7B would be as high or higher in Task A_2as in Task B, despite their re-scaling; this is only true for the data from Experiment 3. Moreover, if memory of Task A_1 had been compromised by Task B, we would expect the percentage errors in Task $A_2$to be as large as they were in Task A_1. Figure 7B shows this was never the case (n=5, t=5.78, p=0.004); even for Experiment 3 alone, the percentage errors were significantly smaller (n=8, t=7.62, p<0.0001). Thus there is little evidence from these experiments for retrograde interference, and strong evidence for anterograde interference moderated by improving adaptation throughout the different experimental phases.

In a related experiment, Bock et al. (2001) used a continuous joystick-tracking task with up-down or right-left mirror reversal of the cursor. From their data, they also argued against interference between short-term memory consolidation mechanisms, and instead proposed a longer-lasting effect based on task incompatibility. Goedert and Willingham (2002) also argued against memory consolidation, by showing that two conflicting tasks always interfere, even with 48 h separation. Like us, and like Seidler (2002), Bock and colleagues (2001) also demonstrated a learning-to-learn effect, in which subjects' performance improved through experience of different task conditions. These data are in line which our current proposal: when the magnitude of the shift in task is taken into account, there is no evidence for catastrophic (retrograde) interference between tasks. The effects can instead be accounted for by anterograde interference, combined with learning to learn.

Finally, we should address the relationship between our experiments and others testing motor consolidation (Brashers-Krug et al. 1995, 1996; Shadmehr and Holcomb 1997, 1999; Shadmehr and Brashers-Krug 1997; Krakauer et al. 1999; Bock et al. 2001; Tong et al. 2002; Goedert and Willingham 2002; Wigmore et al. 2002). The major difference is that we interfered with and tested performance over a short time scale (15 min intervals between acquisition and interference), whereas the other groups used short-term interference (from 5 min to several hours), but then tested its effect the following day, thus measuring the overnight consolidation of the short-term motor memories. In other words, our tests measure only the effects of interference on short-term memory, rather than on consolidation. However, the basic mechanism of motor consolidation is thought to be one of slow consolidation of a fragile short-term memory, over a period of about 5 h (Brashers-Krug et al. 1996) or during REM sleep (Graves et al. 2001; but see Siegel 2001). Hence the disruption and test of short-term memory, whether tested before or after the consolidation process, should give equivalent results, as an intact short-term memory trace is a prerequisite for successful consolidation.

In summary, we have confirmed that the behavioural effects of an interference task on the performance of the opposite motor adaptation task. We show that performance in the interference task is worse than in the initial task, but we do not see evidence of retrograde interference between the two tasks. By considering the relative changes in sensory-motor conditions between the different phases of these experiments, we argue that the results can be explained without retrograde processes, and point instead to retention of the memory of the initial task despite interference.

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