Visuomotor Rotations of Varying Size and Direction Compete for a Single Internal Model in Motor Working Memory

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ABSTRACT

When participants adapt to equal and opposite visuomotor rotations in close temporal proximity, memory of the 1st is not consolidated. The authors investigated whether this retrograde interference depends on the use of equal and opposite rotations. On Day 1, different groups of participants adapted to a −30° rotation followed 5 min later by rotations of +30°, +60°, or −60°. On Day 2, all groups were retested on the −30° rotation. Either retrograde interference (in groups who adapted to rotations of opposite sign on Day 1) or retrograde facilitation (in the remaining group) was observed. In all groups, learning of the 2nd rotation resulted in unlearning of the first, indicating that all visuomotor rotations compete for common working memory resources.

Motor learning and control involve mastering new sensorimotor transformations relating motor output to sensory input. For example, to control a computer mouse, people must learn the kinematic transformation between motion of the mouse over a horizontal pad and motion of the cursor on a vertical monitor. People must also learn the dynamic transformation relating forces applied to the mouse and the resulting movement of the mouse. Thus, for example, people must learn to adapt our force output to the weight of the mouse and the friction between the mouse and mouse pad. Some researchers believe that the ability to learn sensorimotor transformations depends on the acquisition of internal models that capture the mapping between motor commands and desired sensory outcomes (Bhushan & Shadmehr, 1999 ; Conditt, Gandolfo, & Mussa-Ivaldi, 1997 ; Flanagan & Wing, 1997; Johansson & Cole, 1992 ; Jordan & Rumelhart, 1992 ; Kawato, Furukawa, & Suzuki, 1987 ; Krakauer, Ghilardi, & Ghez, 1999 ; Miall & Wolpert, 1996 ; Wolpert, Ghahramani, & Jordan, 1995 ; Wolpert & Kawato, 1998). An internal model may be used to predict the consequences of motor commands (forward model) or to determine the motor commands required to achieve a desired output (inverse model).

In an elegant series of studies, Shadmehr and colleagues (Brashers-Krug, Shadmehr, & Bizzi, 1996 ; Shadmehr & Brashers-Krug, 1997 ; Shadmehr & Holcomb, 1997 ; Shadmehr & Mussa-Ivaldi, 1994) have examined the functional and neural bases of internal model acquisition and consolidation. They assessed how participants adapt to novel force fields applied through a handheld manipulandum during horizontal plane reaching movements. For example, under a rotary viscous force field, the manipulandum generates forces perpendicular to the direction of hand motion and proportional to hand speed. When first performing under such a force field, participants produce altered hand trajectories characterized by curved hand paths and multimodal hand speed profiles. However, after a period of adaptation, participants generate roughly straight-line hand paths and bell-shaped hand speed profiles characteristic of movements observed in the absence of the force field (Shadmehr & Brashers-Krug, 1997 ; Shadmehr & Mussa-Ivaldi, 1994). When the force field is turned off following adaptation, aftereffects are observed such that hand paths are curved in the opposite direction. Such aftereffects demonstrate that participants do not merely stiffen the limb to counter the disturbing forces and suggest, instead, that they learn an internal model of the field (Shadmehr & Mussa-Ivaldi, 1994). Using this internal model, the motor planning system can determine the motor commands and hand forces required to offset the externally imposed force field.

Conditt and colleagues (1997) have provided evidence that participants learn a structured internal model of the force field dynamics and do not use rote memory of the motor commands required to make specific movements. These researchers demonstrated that adaptation to a force field transfers across tasks requiring different patterns of motor commands. For example, if participants adapt to a force field while performing point-to-point reaching movements and then perform a circle drawing task under the same force field, their performance on the drawing task matches that of participants who adapted to the force field while performing the drawing task.

Brashers-Krug and colleagues (Brashers-Krug et al., 1996 ; Shadmehr & Brashers-Krug, 1997) have provided evidence that an internal model of a force field, acquired during training, is gradually consolidated in long-term memory over a period of about 6 hr. During this time, the internal model is fragile and susceptible to interference from newly acquired internal models. Brashers-Krug et al. demonstrated that if participants adapt to a rotary viscous force field and are later tested on the same field, there are large benefits in performance. These benefits appear to persist for as long as 5 months (Shadmehr & Brashers-Krug, 1997). However, if participants adapt to a rotary viscous force field (field A) and then, 5 min later, train on and adapt to a second viscous field with the opposite rotation (field B), there is no improvement on field A when tested either 24 hr or a week later. Brashers-Krug et al. (1996) suggested that this *retrograde interference* is the result of a cancellation of the internal model of field A in working memory caused by learning the competing internal model of field B. In effect, the internal model of field A is unlearned. Consistent with this interpretation, the authors also observed clear *anterograde interference* where initial performance under a force field (A) is impaired if participants first adapt to the opposite force field (B). This impairment arises because, when encountering the new field A, participants start with an internal model adapted for the opposite force field B. If the two force fields are learned more than 6 hr apart, retrograde interference is not observed

and participants can acquire internal models for both fields. Therefore, the inability to recall the first field when the second, opposing field is learned immediately after the first is not a limitation of long-term memory capacity.

Krakauer et al. (1999) have recently demonstrated similar interference and consolidation effects for kinematic transformations. They used a center-out-and-back task in which participants made rapid out and back hand movements to targets located radially from a central start position. The relationship between actual and perceived hand motion was altered using visuomotor rotations. These researchers found that participants who first adapt to a 30° counterclockwise (CCW) rotation and then, 5 min later, adapt to a clockwise 30° rotation, demonstrate no improvement under the CCW 30° rotation when tested 24 hr later. In contrast, participants who train only under the CCW 30° rotation on Day 1 exhibited a clear improvement in performance on Day 2. Building on the results of Brashers-Krug, Shadmehr, and Bizzi (1996) , Krakauer and colleagues argued that successively adapting to two opposing visuomotor rotations leads to unlearning of the internal model of the first rotation and, as a consequence, the first is not consolidated in long-term memory.

Krakauer and colleagues (1999) also demonstrated that kinematic and dynamic transformations do not interfere with one another. They showed that when participants adapt to a 30° visuomotor rotation and then adapt, 5 min later, to a novel dynamic load (created by adding an unseen mass coupled to the upper arm), learning of the rotation is consolidated and there is an improvement in performance on the 30° rotation 24 hr later. Indeed, the level of improvement matches that of participants who only adapt to the 30° rotation on Day 1 and are retested on the 30° rotation a day later. This important result indicates that interference (and lack of consolidation) is not simply a result of learning any two sensorimotor transformations in close temporal proximity. The result also suggests that kinematic and dynamic transformations use independent working memory systems. Further support for the notion that kinematic and dynamic learning are independent comes from the finding that there is no anterograde interference between visuomotor rotations and viscous rotary force fields (Flanagan et al., 1999).

Neurophysiological support for the idea that internal models of sensorimotor transformations are gradually consolidated in long-term memory comes from a study by Shadmehr and Holcomb (1997) in which participants adapted to novel force fields while changes in cerebral blood flow were monitored using positron emission tomography (PET). Shadmehr and Holcomb found that when participants are retested on a force field 5.5 hr after initially adapting to the field, there is a change in activity in ipsilateral anterior cerebellar cortex relative to the late stage of learning when performance under the force field was similar to the performance during recall. This shift in activity suggests that with the passage of time, there is a change in the neural representation of the internal model and that this adjustment accounts for the increased functional stability of the internal model. The findings of Shadmehr and Holcomb add to recent evidence and arguments that the cerebellum plays a central role in the long-term storage of internal models (Imamizu et al., 2000 ; Kawato, 1999 ; Kitazawa, Kimura, & Yin, 1998 ; Tomada, Miyauchi, Imamizu, Yoshioka, & Kawato, 1999 ; Wolpert, Miall, & Kawato, 1998).

Both Brashers-Krug et al. (1996) and Krakauer and colleagues (1999) demonstrated interference effects using equal and opposite sensorimotor transformations (either viscous force fields with rotary forces in opposite directions or visuomotor rotations with opposite signs). The suggestion has been that opposite transformations tend to cancel one another such that learning an internal model for the second leads to an unlearning of the internal model for the first. Here we ask whether the two transformations need to be equal and opposite for interference to occur. We addressed this question by examining interference effects between visuomotor rotations of varying magnitude and either of the same or opposite sign. Different outcomes would be expected depending on the mechanisms assumed to underlie the learning of visuomotor rotations. One possibility is that all visuomotor rotations, regardless of sign and magnitude, compete for common resources in motor working memory. This would predict that learning of any secondary rotation would cause unlearning of the first rotation such that the latter would not be consolidated in long-term memory. On the other hand, it may be that distinct working memory resources can be allocated to visuomotor rotations when they are not equal and opposite. For example, rotation magnitude may provide a powerful contextual cue that enables the allocation of separate working memory resources to different rotations. Finally, it may be that interference is only observed between rotations of different direction.

Experiment 1

The aim of the first experiment was to replicate two key results reported by Krakauer and colleagues (1999) . First, we sought to confirm that when participants adapt to a visuomotor rotation and are retested a day later on the same rotation, they retain much of what they learned. Second, we wanted to confirm that if participants adapt to two equal and opposite visuomotor rotations, one immediately following the other, they do not recall knowledge of the first rotation when tested a day later. Finally, we also tested whether performance on the second rotation (learned on Day 1) was impaired as a result of previously adapting to the first equal and opposite rotation.

Method Participants.

Eighteen undergraduate students volunteered to participate after giving informed consent and received course credit in return. Each participant was randomly assigned to one of three experimental groups (Groups 1—3) with six participants in each group. All participants were right-handed.

Materials.

Participants sat on an adjustable stool at a glass-topped table (Figure 1a) with their right arm supported in a horizontal plane by lightweight aluminum braces mounted on air pucks (Figure 1d). The air pucks, connected to a compressed air supply through flexible plastic tubing, floated on a cushion of air and allowed near-frictionless motion across the tabletop. An opaque shield prevented participants from seeing their arm at all times (Figure 1b). An electromagnetic position sensor (Ascension Technologies, Burlington, VT), taped to the index finger, measured the position of the hand in the horizontal (x, y) plane. A Power Macintosh 7100 was used to sample the position data at a rate of 90 Hz. Specialized software written in LabVIEW (National Instruments Inc., Austin TX) was used for stimulus presentation and data collection.

Procedure.

Participants made out-and-back movements to one of eight targets located radially from a central start position in 45° increments (Figure 1a). The center position was located in the midsaggital plane of the participant and positioned such that the elbow was flexed at 90° when the hand was at the center position. Participants were instructed to move their hands out to the target and back to the start position in one continuous and quick motion and were asked not to make corrective adjustments during the movement. Targets were displayed on a vertical computer monitor positioned at eye level approximately 50 cm in front of the participant. Hand position was represented on the monitor as a cursor. There was a 2:1 mapping between hand and cursor displacement. The diameter of each target was 2 cm in space and 1 cm on the screen. Targets were located 10 cm from the starting position in space and 5 cm from the starting position in terms of cursor distance. In the absence of a visuomotor rotation (referred to as the 0° or null condition), a movement of the hand to the right corresponded to a rightward movement of the cursor, and a movement of the hand away from the body corresponded to an upward motion of the cursor. In some conditions, the mapping between hand motion and cursor motion was altered using a visuomotor rotation about the start position of the hand. For example, under the +30° rotation illustrated in c Figure 1c , the cursor position was rotated +30° relative to hand position. Therefore, the hand would have to move in the 60° direction in order to direct the cursor towards the 90° target. Following the procedure used by Krakauer and coworkers (1999) , we presented targets in a sequence, starting at 0° and continuing in positive, counterclockwise increments of 45°. A *cycle* was defined as eight successive trials from 0° to 315°.

As shown in Table 1 , participants in Group 1 completed 30 cycles under the −30° rotation followed by 30 cycles under the +30° rotation 5 min later. They were then retested under the −30° rotation 24 hr later, completing another 30 cycles. Participants in Group 2 completed 30 cycles under the −30° rotation on Days 1 and 2 and participants in Group 3 completed 30 cycles under the +30° rotation on Day 1. To test for retrograde interference, we compared the performances of Groups 1 and 2 on Day 2 under the −30° rotation. To test for anterograde interference, we compared the performances of Groups 1 and 3 on the +30° rotation.

Data analysis.

The x and y hand position records were differentiated to obtain x and y velocity records. A three-point central difference equation was used for differentiation after first digitally smoothing the position data with a fourth-order, low-pass Butterworth filter using a cut-off frequency of 12 Hz. The velocity of the hand was then calculated as the resultant of the x and y velocities.

For each trial, we determined the movement start and end times, the time and magnitude of peak velocity, the position of the hand cursor at initial peak hand velocity (during the outward movement), and the position of the hand cursor 150 ms after the start. The start and end of the movement were defined as the points at which hand velocity exceeded and dropped below 2 cm/s respectively. The direction of the cursor, relative to the start position, was determined using the position of the cursor at initial peak hand velocity. However, if the peak velocity occurred more than 150 ms after the start, cursor direction was based on the position of the cursor at the 150 ms mark. In this way, we ensured that the direction of the cursor was measured before participants could make corrective movements on the basis of visual feedback. The average time to peak velocity was 177 ms, and the peak velocity occurred after 150 ms in 73% of the trials. For each movement trial, the directional error was taken as the difference between the direction of the target and the direction of the hand cursor. We then computed the median directional error across the eight movements in each cycle. These median directional errors were used in all analyses. Medians were used to reduce the influence of outliers. However, differences between the mean and the median for each cycle were slight (see below). We used analysis of variance (ANOVA) to compare differences within and between groups. For all statistical tests, alpha was set at .05.

Results

Cursor paths produced by a single participant under the −30° rotation for the first and last (30th) cycles are shown in Figure 2 . Although initial directional errors were observed in the first cycle (Figure 2a), directional errors were reduced close to zero by the last cycle (Figure 2b). Figure 2d shows the directional error for each of the 240 trials under the −30° rotation for the same participant, and Figure 2e shows the cycle means and medians. We observed that the mean and median curves were very similar in all cases. Figure 2c shows the tangential velocity profile of the hand for a single trial taken from the last cycle (45° target). The initial peak in the velocity profile (vertical dashed line) occurred just within the 150 ms epoch after movement onset (gray area).

All groups first completed 15 cycles under the null or 0° rotation. We observed an initial bias such that all groups generated small positive directional errors (in the order of 5 to 10°) during initial trials under the 0° rotation. However, in all cases, after several cycles this initial bias was reduced close to zero.

The results of Experiment 1 are summarized in Figure 3 . The figure shows a series of learning curves, each plotting mean directional error as a function of cycle. Separate functions are shown for each Group (1 to 3) and session (A to C). The first and second sessions on Day 1 are labeled A and B, and the session on Day 2 is labeled C. The dots located near the start of each curve represent the average directional error over the first two cycles. These values were used as an index of initial performance.

Participants in Groups 1 and 2 initially carried out 30 cycles under the −30° rotation. During the first few cycles, negative directional errors, slightly smaller in magnitude than the imposed rotation, were observed (see curves labeled G1-SA and G2-SA in Figure 3a). The magnitude of these errors reduced rapidly at first and then decreased more gradually toward zero. As can be seen in b Figure 3b , Group 2 showed appreciable retention of the learning achieved on Day 1. The initial directional error for Group 2 was significantly smaller in magnitude, $F (1, 5) = 44.92$, $p < .05$, on Day 2 ($M = -8.6°$) than on Day 1 ($M = -18.8°$; compare curves G2-SA and G2-SC). Thus, participants in Group 2 were able to recall the information that they had learned the previous day, replicating the results

of Krakauer et al. (1999) .

After completing 30 cycles under the −30° rotation, participants in Group 1 then completed 30 cycles under the +30° rotation. The initial directional error was significantly larger, F (1, 10) = 7.61, p < .05, for Group 1 (M = 41.1°) than for Group 3 (M = 21.6°) who encountered the +30° rotation without first adapting to the −30° rotation. Thus, we observed anterograde interference whereby adapting to the −30° rotation interfered with the performance, 5 min later, on the opposite rotation (+30°).

We also observed retrograde interference. The initial directional error of Group 1 on Day 2 (M = −21.2°) was significantly greater in magnitude, F (1, 10) = 30.37, p < .05, than the initial directional error of Group 2 on Day 2 (M = −8.6°; Figure 3 , 2C). Further evidence of retrograde interference was provided by the lack of improvement from Day 1 when participants in Group 1 returned on Day 2 to complete another 30 cycles under the −30° rotation (Figure 3 , 1C). In fact, the initial error on Day 2 (M = −21.2°) was slightly but reliably greater in magnitude, F (1, 5) = 25.53, p < .05, than on Day 1 (M = −16.3°). Thus, we observed retrograde interference whereby adapting to opposing rotations 5 min apart interferes with the consolidation of first rotation.

We also examined mean directional errors averaged over the last two cycles (Cycles 29 and 30). No significant differences were found between the two −30° rotations performed by Group 1 (Days 1 and 2) or between the second day performances of Groups 1 and 2 under the −30° rotation. Furthermore, no significant difference emerged in the final direction error over the last two cycles between the 30° rotations performed by Groups 1 and 3 on Day 1. Thus, after 30 cycles, rotations of ±30° were learned equally well despite differences in initial performance caused by anterograde or retrograde interference.

Discussion

The main result of Experiment 1 was that when participants adapted to two equal and opposite visuomotor rotations, in close temporal proximity, there was no improvement in performance when participants were tested a day later on the first rotation. This result replicates that of Krakauer and colleagues (1999) . We suggest, as did Krakauer et al., that this lack of consolidation occurred because the two opposing visuomotor rotations compete for the same motor working memory resources. Adapting to the second rotation replaces motor working memory for the first rotation before consolidation can take place. Note that when participants only adapted to a single visuomotor rotation on Day 1, performance on the same rotation was greatly improved when tested on Day 2. Thus, when participants did not adapt to a second, interfering rotation, memory was consolidated in long-term memory.

Experiment 2

The second experiment was identical to the first in all respects except that rotation angles of ±45° were used. The aim of the experiment was to determine whether the results obtained for the ±30° angles generalized to the larger angles. We chose ±45° in order to obtain an angular difference of 90°. This matches the angular difference in Experiment 3 (described below) in which we used rotation angles of −30° and +60° to assess whether interference is observed when rotations are of opposite sign but different magnitude. Thus, we can compare the results of Experiments 2 and 3 without the potential confound of angular difference.

Method

Eighteen undergraduate students participated after giving informed consent and received course credit in return. Each participant was randomly assigned to one of three experimental groups with 6 participants in each group. All participants were right-handed and were naive to the goals of the study. None of the participants had previously participated in experiments on visuomotor adaptation.

As shown in Table 1 , participants in Group 4 experienced the −45° rotation and then the +45° rotation on Day 1 (separated by 5 min). Twenty-four hours later, these participants were retested on the −45° rotation. Participants in Group 5 only experienced the —45° rotation on Day 1 and were retested on the −45° rotation a day later. Participants in Group 6 experienced the +45° rotation on Day 1. The general procedure and the data analysis were the same as in Experiment 1.

Results

Participants in Group 5, who encountered the −45° rotation on Days 1 and 2, showed substantial retention of learning across days (Figure 4b). The initial directional error was significantly smaller in magnitude, F (1, 5) = 9.63, p < .05, on Day 1 (M = −9.8°) than on Day 2 (M = −28.9°). In contrast, participants in Group 4, who encountered the −45° rotation immediately followed by the +45° rotation on Day 1, showed no retention of the −45° rotation on Day 2 (Figure 4a ; compare curves G4-SA and G4-SC). For Group 4, the initial errors under the −45° rotations on Days 1 (M = −25.4°) and 2 (M = −32.9°) were not significantly different, F (1, 5) = 4.72, ns . Moreover, the magnitude of the initial error observed under the −45° rotation on Day 2 was significantly larger, F (1, 10) = 19.39, p < .05, for Group 4 than for Group 5 (M = −9.8°; Figure 4 , compare curves G4-SC and G5-SC). Thus, we observed clear evidence of retrograde interference.

We also observed anterograde interference. Initial errors under the +45° rotation were greater in magnitude when participants had

adapted to the −45° rotation immediately before (Figure 4 ; compare curves G4-SB and G6-SA). The initial errors with (M = 62.3°) and without (M = 38.3°) prior exposure to the −45° rotation were significantly different, F (1, 10) = 70.41, p < .05.

Discussion

The results of Experiment 2 demonstrate that the patterns of interference observed between equal and opposite visuomotor rotations of magnitude 30° (see Experiment 1 and Krakauer et al., 1999) are also observed for equal and opposite visuomotor rotations of magnitude 45°. Thus, our results suggest that equal and opposite visuomotor rotations compete for common working memory resources regardless of rotation angle.

Experiment 3

The aim of the third experiment was to determine whether the powerful retrograde and anterograde interference effects, described previously (Krakauer et al., 1999) and replicated above for equal and opposite visuomotor rotations, are also observed when rotations of opposite sign but different magnitude are involved.

Method

Thirteen undergraduates participated after giving informed consent. They received course credit in return. Each participant was randomly assigned to one of two experimental groups; Group 7 had 6 participants, and Group 8 had 7 participants. All participants were right-handed, and none had previously participated in a similar experiment. The participants were naive to the goals of the study.

As shown in Table 1 , participants in Group 7 experienced the −30° rotation followed by the +60° rotation on Day 1. Twenty-four hours later, these participants were retested under the −30° rotation. Participants in Group 8 experienced the +60° rotation on Day 1. We assessed retrograde interference by comparing the results of Groups 7 and 2 on the −30° rotation tested on Day 2. To test for anterograde interference, we compared the performances of Groups 7 and 8 on the +60° rotation experienced on Day 1. The general procedure and the data analysis were the same as in Experiments 1 and 2.

Results

We compared the initial directional errors of Group 7 and Group 8 under the 60° rotation and found clear evidence of anterograde interference. The magnitude of the initial error for Group 7 (M = 71.7°) was significantly greater, F (1, 11) = 30.84, p < .05, than for Group 8 (M = 56.3°; Figure 5 , compare curves G7-SB and G8-SA). Thus, learning two rotations of opposite sign 5 min apart interfered with initial performance on the second rotation, even when the rotations angles were not equal in magnitude.

We also observed retrograde interference. When participants in Group 7 returned on Day 2, their initial directional error under the −30° rotation (M = −23.6°) was not significantly different, F (1, 5) = 1.40, ns , than on Day 1 (M = −19.9°) when they first encountered the same rotation (Figure 5 , compare curves G7-SA and G7-SC). Thus, learning of the −30 rotation on Day 1 was not consolidated in memory when participants were exposed to an opposite, but not equal, rotation immediately following the learning. Clear evidence of retrograde interference was provided by comparing the initial directional errors of Groups 7 and 2 on Day 2 (Figure 5 , compare curves G7-SC and G2-SC). The initial error for Group 7 (M = −23.6°) was significantly greater in magnitude, F (1, 10) = 18.23, p < .05, than for Group 2 (M = −8.6°).

We also compared the initial directional error on Day 2 of Groups 7 and 1 and found no significant difference, F (1, 10) = 0.37, ns . Thus, the magnitude of the second (opposite) rotation on Day 1 did not appear to affect the initial directional error on Day 2 (compare curve G7-SC in Figure 5 with curve G1-SC in Figure 3). If participants recalled the second rotation learned on Day 1 when starting out on Day 2, the initial directional error should have been greater for Group 7 than Group 1. However, it should be noted that Group 7 did not adapt as fully to the 60° rotation as did Group 1 to the 30° rotation (compare curves G7-SB and G1-SB in Figure 5). The final directional error observed for Group 7 on the second +60° rotation (M = 23.0°) was significantly greater, F (1, 10) = 5.72, p < .05, than the final directional error observed for Group 1 on the second +30° rotation (M = 7.8°). Thus, the fact that Group 7 did not exhibit greater initial errors on Day 2 than Group 1 may be due to poorer adaptation to the second rotation on Day 1. The difference between Groups 1 and 7 in the final directional error on the second rotation on Day 1 was not simply due to differences in the magnitude of the rotations per se. There was no significant difference, F (1, 11) = 0.33, ns , between the final errors observed for Group 1 on the +30° rotation and Group 8 on the +60° rotation (M = 10.9°). Thus, the lack of full adaptation observed for Group 7 on the +60° rotation appears to be due to the combination of anterograde interference from the previously learned —30° rotation and the magnitude of the rotation.

Discussion

The results of Experiment 3 demonstrate that interference can occur between two visuomotor rotations of opposite sign even when the rotations are of different magnitude. In particular, participants who adapted to 30° rotation in one direction and then adapted, after a 5-min break, to a 60° rotation in the opposite direction, did not exhibit improved performance on the 30° rotation when tested a day later. Thus, adaptation to the opposite 60° rotation appeared to overwrite the internal model acquired for the 30° rotation before it could be consolidated in long-term memory. The results suggest that opposing visuomotor rotations compete for common motor working memory resources regardless of their magnitudes.

Experiment 4

The aim of the fourth experiment was to examine interference and facilitation effects when learning rotation angles of equal sign but unequal size.

Method

Twenty-four undergraduate students participated after giving informed consent and received course credit in return. Each participant was randomly assigned to one of four experimental groups with six participants in each group. All participants were naive with respect to the goals of the study, were right-handed, and none had previously participated in an experiment on visuomotor adaptation.

As shown in Table 1 , participants in Group 9 experienced the —30° rotation and then the −60° rotation on Day 1. Twenty-four hours later, participants in Group 9 were retested on the −30° rotation. Participants in Group 10 only experienced the −60° rotation on Day 1. To test for anterograde effects, we compared the performances of Group 9 and 10 on the −60° rotation on Day 1. Retrograde effects were assessed by comparing the results of Groups 9 and 2 on the −30° rotation tested on Day 2.

We reasoned that participants in Group 9 might perform well under the −30° rotation on Day 2 if they started with an internal model adapted to the −60° rotation they last experienced on Day 1. If so, the good performance on Day 2 would not provide evidence for consolidation of the −30° rotation learned on Day 1. To distinguish between these possibilities, we included two additional control groups of participants. Group 11 experienced the −60° rotation followed by the −30° rotation on Day 1. Group 12 experienced the −60° rotation on Day 1 and the −30° rotation on Day 2. The general procedure and the data analysis were the same as in the previous three experiments.

Results

Group 9 was included in the experiment so that we could examine the patterns of interference, and possible facilitation, between different visuomotor rotations of the same sign. To examine anterograde effects, we compared Group 9's performance under the −60° rotation with that of Group 10 who performed under the −60° rotation without first adapting to the −30° rotation (a Figure 6a , compare curves G9-SB and G10-SA). The magnitude of the initial directional error was significantly smaller, F (1, 10) = 5.16, p < .05, for Group 9 (M = −15.9°) than for Group 10 (M = −36.6°). Thus, initial performance under the −60° rotation was facilitated by adapting to the −30° rotation immediately before.

Adapting to the −60° rotation after the −30° rotation on Day 1 facilitated subsequent performance under the −30° rotation on Day 2 (a Figure 6a , compare curves G9-SA and G9-SC). For Group 9, the magnitude of the initial error under the −30° rotation was reliably smaller, F (1, 5) = 42.72, p < .05, on Day 2 (M = 0.8°) than on Day 1 (M = −15.9°). Direct evidence of retrograde facilitation was provided by comparing the initial errors on Day 2 of Groups 9 and 2. The magnitude of the initial error was significantly larger, F (1, 10) = 40.27, p < .05, for Group 2 (M = −8.6°) who did not encounter the intervening −60° rotation on Day 1.

At first glance, it would appear that the results obtained when learning rotations of the same sign are very different than those obtained when learning rotations of opposite sign (Experiments 1—3). In particular, learning of the −60° rotation immediately following the −30° rotation did not interfere with subsequent recall, 24 hr later, of the −30° rotation. In fact, learning of the −60° rotation appeared to facilitate recall of the −30° rotation. This latter finding is surprising. Why would performance under the −30° rotation be better after learning the −30° and −60° rotations on Day 1 (Group 9) than when only learning the −30° rotation?

One possibility is that participants in Group 9 effectively learned a −30° rotation twice on Day 1. When these participants were exposed to the −60° rotation after first adapting to the −30° rotation, the −60° became a −30° rotation relative to the first rotation. Thus, in effect, the participants were exposed to two relative −30° rotations in a row. This double learning may explain the better recall of the −30° rotation on Day 2. However, one flaw with this idea is that adaptation to the −60° rotation (the second relative rotation of −30° for Group 9) was no better than the initial adaptation to the −30° rotation (a Figure 6a , compare curves G9-SA and G9-SB). The double-learning idea predicts that the directional error should have been smaller under the second relative rotation (Group 9, Session B) than the first (Group 9, Session A).

A second possible explanation for the small initial errors observed on Day 2 for Group 9 is that the participants may have consolidated the −60° rotation, as opposed to the −30° rotation, and then partially recalled the −60° rotation on Day 2. Partial recall of the larger rotation might result in more or less perfect initial performance under the −30° rotation. Evidence of such partial recall is provided from Groups 2 and 5 who were exposed to the same −30° and −45° rotations on Days 1 and 2 respectively. Inspection of Figures 3b and 4b reveals that, on Day 2, initial errors were clearly smaller in magnitude than on Day 1, but they were still substantial. The initial error

under the −30° rotation for Group 2 on Day 2 was −8.6°, and the initial error under the −45° rotation for Group 5 on Day 2 was −9.8°.

A final possibility is that participants recalled the −60° rotation but then rapidly scaled the rotation down to −30°. If so, then such rapid scaling would appear to only apply to scaling down a learned rotation and not to scaling up. When participants in Group 9 encountered the −60° rotation after adapting to the −30° rotation, they did not adapt rapidly.

To test among these alternate explanations, we tested two additional groups of participants. Groups 11 and 12 encountered the −60° rotation followed by the −30° rotation after either 5 min (Group 11) or 24 hr (Group 12). We hypothesized that Group 12 would exhibit almost perfect performance under the −30° rotation on Day 2. That is, we predicted that the initial directional error would be close to zero. This would provide evidence supporting the idea of partial recall because Group 12 only learned the −60° rotation on Day 1 as opposed to two consecutive relative rotations of −30° (see Group 9). This was found to be the case. The initial direction error for Group 12 under the −30° rotation on Day 2 (M = 0.7°) was close to zero (see Figure 6b) and not significantly different, F (1, 10) < 0.01, ns , from the initial error for Group 9 under the −30° rotation on Day 2 (M = 0.8°).

Evidence against the notion that participants can rapidly scale down a learned rotation of —60° to deal with a smaller rotation of −30° is provided by comparing the initial directional errors of Groups 11 and 12 under the −30° rotation. The magnitude of the initial error was significantly greater, F (1, 10) = 8.08, p < .05, for Group 11 (M = 8.1°).

Discussion

The results of the last experiment indicate that visuomotor rotations of different magnitude compete for common resources in motor working memory even when they are of the same sign. Participants who successively adapted to a 30° and then a 60° rotation (of the same sign) on Day 1 and participants who only adapted to the 60° rotation on Day 1 exhibited similar performance when tested a day later on the 30° rotation. Thus, initial adaptation to the 30° rotation on Day 1 had no apparent effect on what was consolidated in memory. This result suggests that the internal model acquired in working memory during adaptation to the 30° rotation was overwritten by subsequent adaptation to the 60° rotation.

General Discussion

The learning of new motor tasks is thought to involve the acquisition of internal models that encode the mapping between motor output and desired sensory outcomes (Wolpert, 1997 ; Wolpert et al., 1995). Shadmehr and Brashers-Krug (1997) have proposed a two-stage model of such motor learning. The initial stage involves the acquisition, during practice, of an internal model in motor working memory. The second stage involves the more gradual consolidation of an internal model in long-term memory. Experiments by Shadmehr and colleagues (Shadmehr & Brashers-Krug, 1997 ; Shadmehr & Mussa-Ivaldi, 1994) and Krakauer and colleagues (1999) have demonstrated that the internal model in working memory is short-lived and fragile in that it can be interfered with by new learning. In contrast, the internal model in long-term memory is more stable and is not affected by novel learning.

According to Shadmehr and Brashers-Krug (1997) , when two opposing force fields are learned closely together in time, the learning of the second force field undoes the learning of the first because it uses, and retunes, the same neural resources in working motor memory. As a consequence, the internal model of the first force field is not consolidated in long-term memory. A similar pattern of retrograde interference has been demonstrated for learning of equal and opposite visuomotor rotations (Krakauer et al., 1999).

Our results are consistent with the two-stage model outlined by Shadmehr and Brashers-Krug (1997) . Moreover, they extend the model by showing, in the context of visuomotor rotations, that all transformations compete for the same working memory resources regardless of sign or magnitude. The results of the first three experiments showed that the learning of two successive visuomotor rotations of opposite sign results in both anterograde interference and complete retrograde interference regardless of whether rotation magnitudes were equal or different. Thus, cancellation of the first internal model in working memory does not require strict cancellation in terms of rotations (i.e., equal and opposite rotations).

In the fourth experiment, we observed both anterograde and retrograde facilitation between rotations of the same sign but different magnitude (−30° and −60°). The anterograde facilitation is predicted by a model of learning that assumes that all visuomotor rotations compete for common working memory resources. Participants would first acquire an internal model of the −30° rotation in working memory and then apply this model to the —60° rotation. Because the −30° rotation is closer to −60° than the normal starting point (0° rotation), anterograde facilitation is observed. The retrograde facilitation is more difficult to explain within the context of the common working memory model. According to this scheme, the internal model of the initial −30° rotation should be replaced by an internal model for the subsequently learned −60° rotation. If the latter is then recalled when the −30° rotation is encountered 24 hr later, neither facilitation nor interference should be observed because the difference between −60° and −30° is equivalent to the difference between −30° and 0°. This reasoning assumes that the −60° rotation is fully recalled on the second day. However, our results indicated that participants do not fully recall a learned rotation, even when it was the only rotation learned the previous day (see also Krakauer et al., 1999). If one accepts the notion that recall of a learned internal model results in only partial initial adaptation a day later, then the results of the fourth experiment are also consistent with the idea that all visuomotor rotations compete for a single internal model in working motor memory.

In cases in which participants were exposed to two opposing rotations on Day 1 (−30° followed by either 30 or 60°), we observed that the magnitude of the second rotation (30 or 60°) did not reliably affect the initial error under the −30° rotation on Day 2. This result appears to be inconsistent with the claim that, on Day 2, participants (partially) recall the last rotation they were exposed to on Day 1. If this were the case, then we would expect larger initial errors in the Group last exposed to the 60° rotation on Day 1. However, we also observed that participants last exposed to the 60° rotation on Day 1 did not fully adapt. This lack of full adaptation may explain why these participants exhibited initial errors on Day 2 that were similar to those exhibited by participants last exposed to the 30° rotation on Day 1 and who adapted more fully.

Although our results suggest that successively learned visuomotor rotations compete for a single internal model in working memory, this does not imply that, under suitable conditions, motor working memory is incapable of maintaining internal models of two visuomotor transformations. Cunningham and Welch (1994) have shown that people can learn to switch between two different visuomotor maps–with and without a visuomotor rotation of 108° –if they practice them in alternating blocks of trials and are provided with adequate cues. Similarly, using a target throwing task, Martin, Keating, Goodkin, Bastian, and Thach (1996) have shown that people can learn to accurately switch between two visuomotor transformations (with and without wedge prism glasses) if they throw alternately, with and without prisms, over a period of 6 weeks.

Previous work on learning of novel force fields (Brashers-Krug et al., 1996 ; Shadmehr & Brashers-Krug, 1997 ; Shadmehr & Holcomb, 1997) has shown that the consolidation of an internal model in long-term memory is largely completed within 5 to 6 hr. This work has also shown that there is a corresponding decay of the internal model in working memory over this period. However, both long-term memory consolidation and short-term memory decay may continue for longer periods up to and exceeding 24 hr (Shadmehr & Brashers-Krug, 1997). To our knowledge, corresponding data for visuomotor transformation have not been reported. In this regard, it is interesting to note that participants in Group 1 generated initial directional errors that were slightly but significantly larger in magnitude under the −30° rotation on Day 2 than on Day 1. This slight increase in error magnitude may have been due to anterograde interference from the 30° rotation learned 24 hr earlier and still present, in small measure, in working memory. Note that a similar trend was observed for Group 4 (with −45° rotations), but the difference did not reach significance.

Recall of a learned internal model of a visuomotor rotation is the culmination of a series of processes including perception of the task, integration of sensory information, activation of the motor memory, and finally, action (Shadmehr & Brashers-Krug, 1997). Consequently, poor performance in a test of recall may not simply imply that the motor memory component has been affected. Poor recall can also be attributed to the inaccessibility of the stored information, rather than its loss (Koppenaal, 1963 ; Squire, Slater, & Miller, 1981). For example, Capaldi and Neath (1995) have proposed that forgetting is a problem of discrimination. According to this view, during learning, the organism processes not only the material to be learned, but also cues or stimuli associated with that material. As a result, when learning a task, individuals process a multidimensional complex of stimuli. Forgetting occurs if the stimulating conditions at test do not sufficiently discriminate between the desired memories and some other competing memories. Consequently, forgetting is seen as a performance deficit resulting from inadequate stimulus conditions.

Although ample evidence suggests that various contextual cues can be used effectively to recall learned internal models of visuomotor transformations (Cunningham & Welch, 1994 ; Ghahramani & Wolpert, 1997 ; Vetter & Wolpert, 2000) and force fields (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996), there are several arguments against the notion that the retrograde interference observed here is due to an inability to discriminate the appropriate context rather than an inability to consolidate. First, although the different visuomotor rotations were performed in a similar environment and were not linked to explicit cues (such as a color or auditory tone), the very act of moving provides continuous proprioceptive and visual feedback that is unique to a specific rotation. This feedback can provide a powerful cue for recalling the appropriate internal model for a particular rotation after an initial movement is generated. Wolpert and Kawato (1998 ; Kawato & Wolpert, 1998) have suggested that when performing motor tasks, the brain makes multiple predictions of sensory outcomes on the basis of multiple learned internal models. By comparing these predictions with actual sensory feedback, the motor controller can select the most appropriate internal model for the task (Blakemore, Goodbody, & Wolpert, 1998).

Further evidence against the hypothesis that retrograde interference is due to an inability to discriminate context comes from the demonstration that participants can learn and recall two opposing force fields provided they are not learned within 5 hr of each other (Shadmehr & Brashers-Krug, 1997). Here the context (i.e., experimental setting) is the same for both force fields and yet participants can rapidly select and recall the appropriate internal model after a few movements in a given force field. Taken altogether, these results indicate that retrograde interference is caused by an inability to consolidate an internal model in long-term memory rather than an inability to recall.

In summary, the results of this study support a two-stage model of motor learning where the first stage involves the formation of an internal model in working motor memory and the second involves consolidation of an internal model in long-term memory (Shadmehr & Brashers-Krug, 1997). The results also indicate that all visuomotor rotations compete for a single internal model in working motor memory. As a result, when two different visuomotor rotations are learned in close temporal proximity, the second replaces the first such that the first is lost before it can be consolidated in long-term memory.

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Table 1. Visuomotor Rotations Experienced by the Experimental Groups

Table 1

Visuomotor Rotations Experienced by the Experimental Groups

| Experiment and group | Day 1 | | Day 2 |
	Session A	Session B	Session C
Experiment 1			
Group 1	−30°	30°	−30°
Group 2	−30°		−30°
Group 3	30°		
Experiment 2			
Group 4	−45°	45°	−45°
Group 5	−45°		−45°
Group 6	45°		
Experiment 3			
Group 7	−30°	60°	−30°
Group 8	60°		
Experiment 4			
Group 9	−30°	−60°	−30°
Group 10	−60°		
Group 11	−60°	−30°	
Group 12	−60°		−30°

Note. The first and second sessions on Day 1 are labeled A and B, and the session on Day 2 is labeled C. For all groups who completed two sessions on Day 1, the time delay between the end of Session A and the start of Session B was 5 min. On Day 1, but not Day 2, all participants in all groups first completed 15 cycles under the 0° rotation. For all the other visuomotor rotations, participants completed 30 cycles.

Figure 1. Experimental apparatus. A: Participants sat at a table and moved one of their arms over a glass surface to one of eight targets located radially from the central start position. B: The targets, start position, and a cursor representing hand position were presented on a vertical monitor positioned in front of the participant. A shield blocked vision of the arm. C: Visuomotor rotations altered the mapping between hand direction and cursor direction. Under a 30° rotation, for example, the direction of the cursor was rotated counterclockwise (CCW) from the direction of the hand. D: The arm was supported by lightweight air sleds providing near-frictionless motion of the arm over the glass tabletop. The position of the hand in the horizontal (x, y) plane was recorded with an electromagnetic sensor.
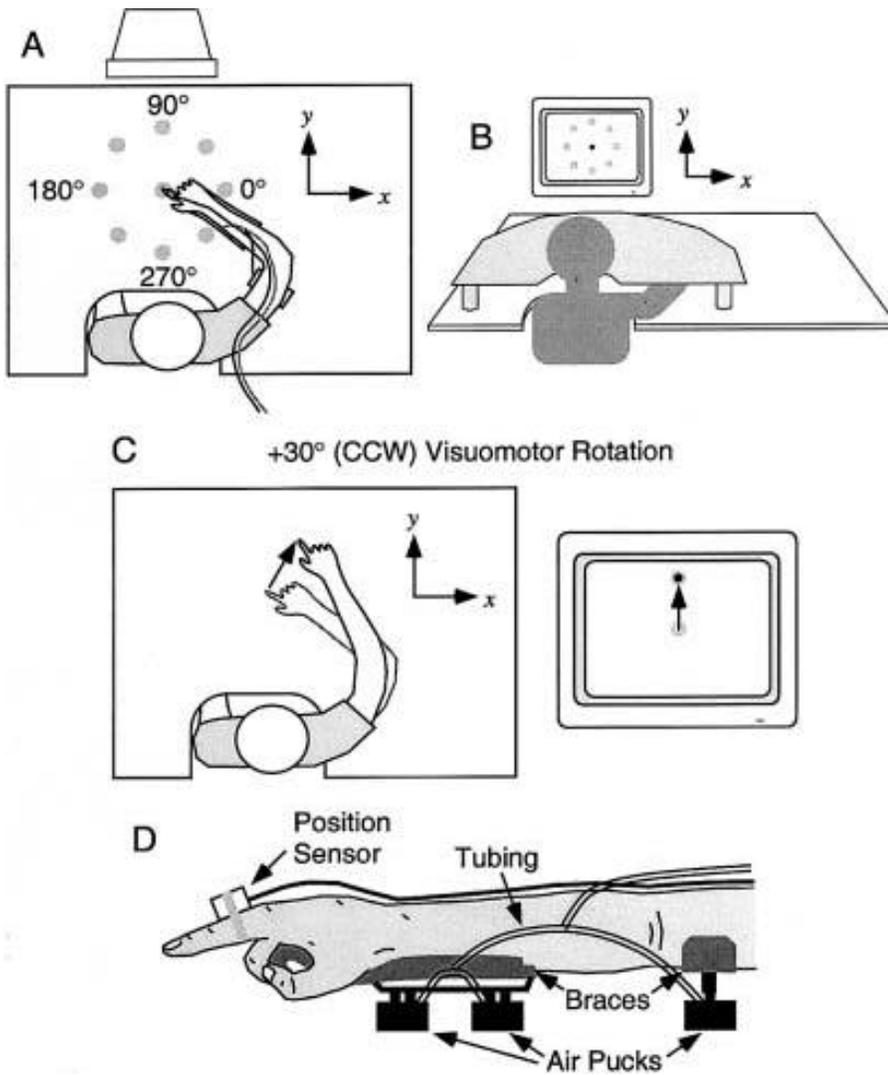
Figure 2. Cursor paths and directional errors from single trials. A: Cursor paths from the first eight movements (Cycle 1) under the −30° rotation (data from a single participant). For clarity, two movement paths (directed to opposing targets) are shown in each plot. B: Cursor paths from the last eight movements (232 to 240; Cycle 30). C: Tangential velocity profile of the hand for the last movement to the 45° target. The gray bar is aligned at movement onset and is 150 ms wide. Movement direction was measured at the first velocity peak (vertical dashed line) or at 150 ms after movement onset, whichever occurred first. D: Directional errors for all Participant 1A's movements as a function of cycle. E: Mean (solid) and median (dashed) errors for eight movements per cycle plotted as a function of cycle. The gray area represents ±1 SD .
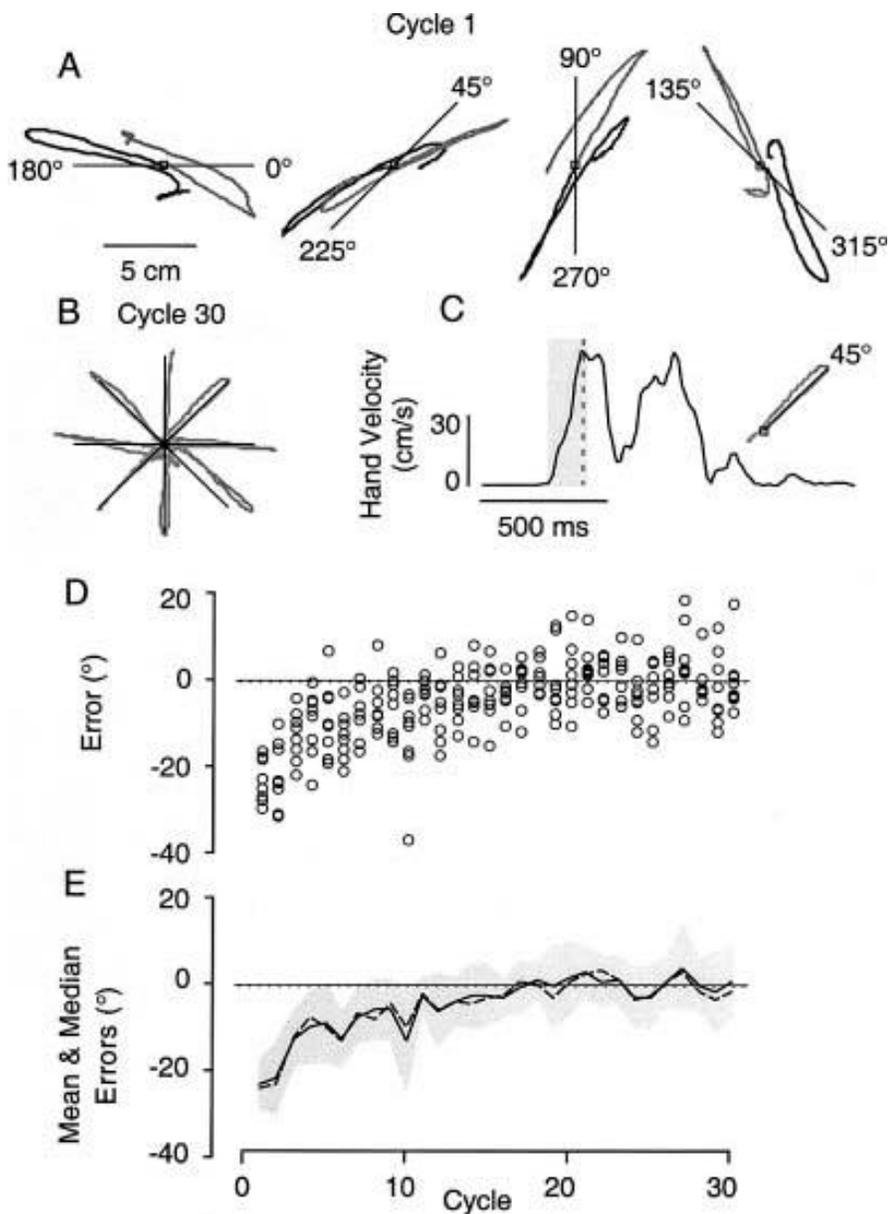
Figure 3. Learning curves illustrating anterograde and retrograde interference effects between equal and opposite visuomotor rotations of 30°. Each curve shows mean direction error as a function of cycle for one group and session. The labels to the left of the curve indicate the group (G) and session (S). Light gray areas represent ±1 SE. The filled circles at the start of each curve represent the mean directional error over the first two cycles, and the vertical lines attached to the circles represent +1 SE. The vertical brackets indicate comparisons carried out between the mean errors over the first two cycles; a double line indicates a reliable difference ($p < .05$). The dotted horizontal lines represent zero directional error. Two panels (A and B) are used so that the different learning curves can be distinguished. The learning curve for G2-SC is shown in both panels because it was used in two comparisons.
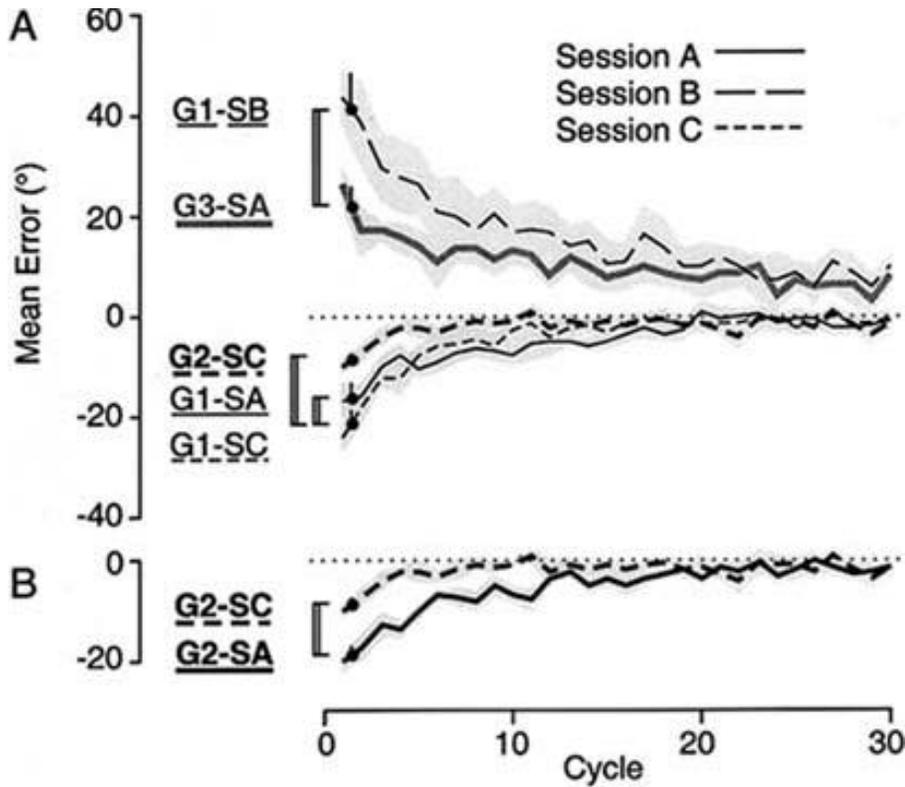
Figure 4. Learning curves illustrating anterograde and retrograde interference effects between equal and opposite visuomotor rotations of 45°. Each curve shows mean direction error as a function of cycle for one group (G) and session (S). Light gray areas represent ±1 *SE* . The filled circles at the start of each curve represent the mean directional error over the first two cycles, and the vertical lines attached to the circles represent +1 *SE* . The vertical brackets indicate comparisons carried out between the mean errors over the first two cycles; a double line indicates a reliable difference ($p < .05$). The dotted horizontal lines represent zero directional error. Two panels (A and B) are used so that the different learning curves can be distinguished. The learning curve for G5-SC is shown in both panels.
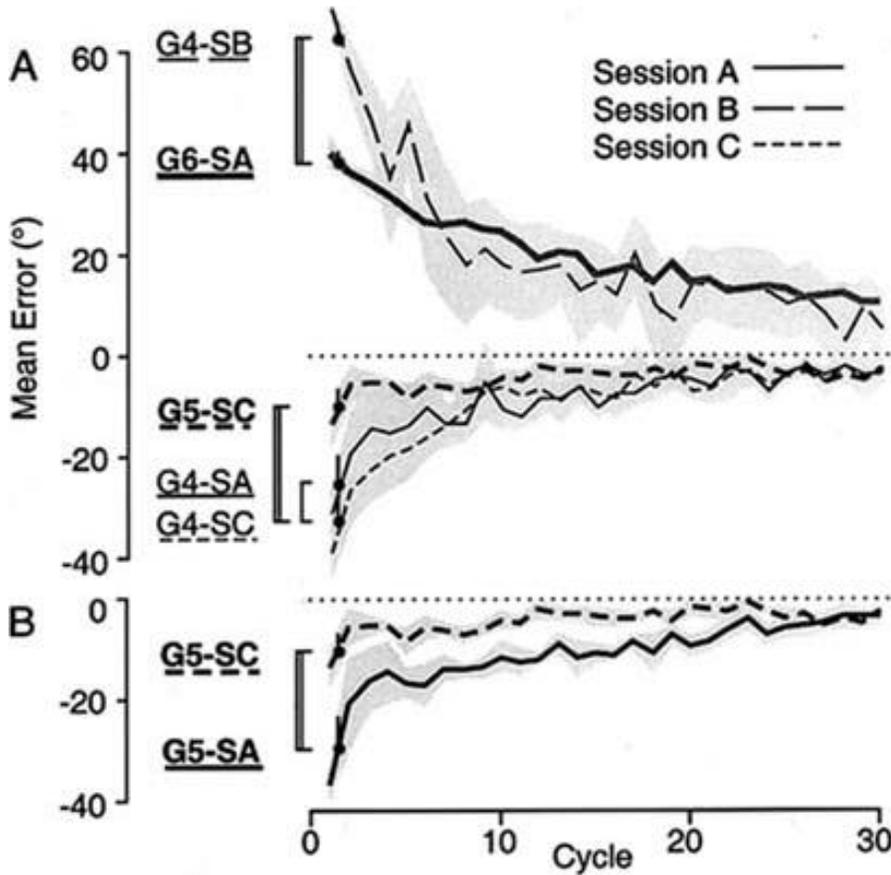
Figure 5. Learning curves illustrating anterograde and retrograde interference effects between opposite visuomotor rotations of different magnitude. Each curve shows mean direction error as a function of cycle for one group (G) and session (S). Light gray areas represent ± 1 *SE* . The filled (open) circles at the start (end) of each curve represent the mean directional error over the first (last) two cycles, and the vertical lines attached to the circles represent $+1$ *SE* . The vertical brackets indicate comparisons carried out between the mean errors over the first two cycles; a double line indicates a reliable difference ($p < .05$). The dotted horizontal line represents zero directional error.
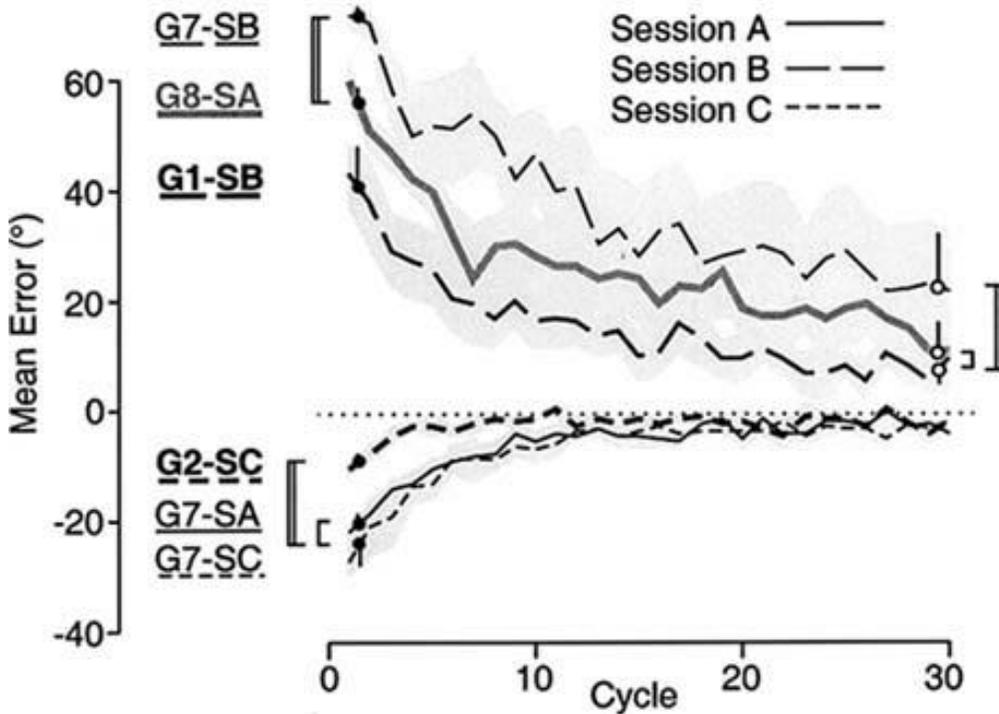
Figure 6. Learning curves illustrating anterograde and retrograde interference effects between visuomotor rotations of the same sign. Each curve shows mean direction error as a function of cycle for one group (G) and session (S). Light gray areas represent ± 1 *SE* . The filled circles at the start of each curve represent the mean directional error over the first two cycles, and the vertical lines attached to the circles represent +1 *SE* . An open circle is used for Group 9, Session B for clarity. The vertical brackets indicate comparisons carried out between the mean errors over the first two cycles; a double line indicates a reliable difference ($p < .05$). The dotted horizontal lines represent zero directional error. Two panels (A and B) are used so that the different learning curves can be distinguished.