

Task-Specific Internal Models for Kinematic Transformations

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Tong, Christine and J. Randall Flanagan. Task-specific internal models for kinematic transformations. *J Neurophysiol* 90: 578–585, 2003; 10.1152/jn.01087.2002. Numerous studies of motor learning have focused on how people adapt their reaching movements to novel dynamic and visuomotor perturbations that alter the actual or visually perceived motion of the hand. An important finding from this work is that learning of novel dynamics generalizes across different movement tasks. Thus adaptation to an unusual force field generalizes from center-out reaching movements to circular movements (Condit et al. 1997). This suggests that subjects acquired an internal model of the dynamic environment that could be used to determine the motor commands needed for untrained movements. Using a task interference paradigm, we investigated whether transfer across tasks is also observed when learning visuomotor transformations. On day 1, all subjects adapted to a +30° rotation while making center-out-and-back reaching movements. After a delay of 5 min, different groups of subjects then adapted to a –30° rotation while performing either a continuous tracking task, a figure-eight drawing task, or the center-out-and-back reaching task. All subjects were then retested the next day on the +30° rotation in the reaching task. As expected, subjects who experienced the opposing rotations while performing the same reaching tasks showed no retention of learning for the first rotation when tested on day 2 (Krakauer et al. 1999). In contrast, such retrograde interference was not observed in the two groups of subjects who experienced the opposing rotations while performing different tasks. In fact, their performance on day 2 was similar to that of control subjects who never experienced the opposite rotation. This lack of interference suggests that memory resources for visuomotor rotations are task specific.

INTRODUCTION

From the perspective of the motor system, the acquisition of new skills is primarily concerned with learning novel mappings between motor commands and their sensory consequences. Knowledge of such a mapping—referred to as an internal model—is required to estimate the motor commands required to achieve desired outcomes, to generate the sensory predictions needed to assess whether actions are unfolding as expected, and to distinguish self- and externally produced sensations (Blakemore et al. 1998; Flanagan and Wing 1997; Johansson and Cole 1992; Jordan and Rumelhart 1992; Kawato et al. 1987; Krakauer et al. 1999; Lackner and DiZio 1994; Miall and Wolpert 1996; Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995; Wolpert and Flanagan 2001).

Learning a novel sensorimotor transformation involves two stages. The first stage involves the acquisition of an internal

model in motor working memory through practice. In the second stage, this information is consolidated into long-term memory (Brashers-Krug et al. 1996; Muellbacher et al. 2002). The preconsolidation internal model in working memory is susceptible to interference by new learning and thus may be considered to be fragile. When people successively adapt their reaching movements to two opposing visuomotor rotations (Krakauer et al. 1999; Wigmore et al. 2002; see also Bock et al. 2001) or force fields applied to the hand (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997) or arm (Krakauer et al. 1999), the first is not consolidated and cannot be recalled later. This retrograde interference is complemented by anterograde interference—initial performance on the second transformation is impaired by adaptation to the first. These results suggest that opposing transformations compete for common working memory resources.

Recent studies in motor learning of novel dynamics have investigated whether interference between opposing force fields can be eliminated or attenuated by altering either context or the task performed under the two fields. Gandolfo and colleagues (1996) examined people's ability to learn opposing viscous rotary force fields presented in alternating blocks of trials. In the absence of visual cues, people were unable to learn the force fields. Although adaptation was observed within a given block, the adaptation was not retained across blocks. Learning was not improved by the provision of arbitrary color or kinesthetic cues produced by changing background lighting or thumb position for each force field. Arbitrary color, auditory, and kinesthetic cues have also been shown to be rather ineffective when adapting to conflicting visuomotor transformations (Cunningham and Welsh 1994; Martin et al. 1996; Seidler et al. 2001). In contrast, Gandolfo et al. (1996) demonstrated that changing grasp posture *does* lead to independent learning of the two fields. In contrast to the arbitrary color and kinesthetic cues, this latter manipulation alters the motor commands required to perform the task. This suggests that the internal model captures the mapping between motor commands and sensory consequences that is determined by both the force field and arm posture rather than the force field per se.

Condit and colleagues (1997) tested whether different tasks, performed under the same rotary viscous force field, share the same internal model in motor working memory. They showed that adaptation to a force field transferred fully from a center-out reaching task to a circle-drawing task. Thus the internal

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model developed for the first task could be exploited when performing the second. Because the temporal sequence of motor commands needed to perform the two tasks are very different, these results provide strong evidence against the idea that adaptation to a force field involves rote memorization of the motor commands required to perform a specific task. Rather, the results indicate that dynamic learning involves the learning of mappings between states visited by the arm and the resulting force (i.e., a state-dependent force field).

The results of Conditt et al. (1997) demonstrate anterograde facilitation across tasks performed under the same sensorimotor transformation. However, the question arises whether retrograde interference would also be observed between opposing sensorimotor transformations experienced in different tasks. That is, when opposing transformations are experienced with different tasks, will the unlearning of the first transformation—observed when the task is not altered (Brashers-Krug et al. 1996; Krakauer et al. 1999)—still occur? The aim of the current study was to assess this question using opposing visuomotor rotations and three different tasks: a center-out-and-back reaching task, a target-tracking task, and a drawing task that involved copying a figure-eight template. Four groups of subjects first experienced a counterclockwise visuomotor rotation on day 1 while performing the reaching task. Three of the groups then experienced, 5 min later, an opposing clockwise rotation while performing either the reaching task, the tracking task, or the drawing task. All four groups were then retested the next day on the counterclockwise rotation in the reaching task. We hypothesized that opposing rotations experienced in different tasks would be independently learned. Thus we predicted that exposure to the clockwise rotation in the tracking and drawing tasks (but not the reaching task) would not interfere with retention of learning of the counterclockwise rotation in the reaching task.

METHODS

Participants

Sixty undergraduate students gave informed consent to participate in this study in exchange for bonus course credit. Participants were randomly assigned to one of eight experimental groups with eight participants in each of groups 1 to 6 and six participants each in two additional control groups (groups 7 and 8). All participants were right-handed and reported corrected-to-normal vision.

Materials

Participants performed each task while sitting on an adjustable stool at a glass-topped table (Fig. 1A). To reduce fatigue, their arms were supported by lightweight aluminum braces mounted on air pucks (Fig. 1B). These air pucks were connected to a compressed air supply and created an air cushion to minimize friction across the horizontal work surface. Hand position was measured using an electromagnetic position sensor (Ascension Technologies, Burlington, VT) that was taped to each participant's index finger. The position data were sampled at 100 Hz using software written in LabVIEW (National Instruments, Austin, TX). The visual stimuli were projected on a rear projection screen (with approximately a 20-ms delay) and seen by the participants as a reflected image in a semisilvered mirror (Fig. 1A). Participants could not see their arm through the mirror.

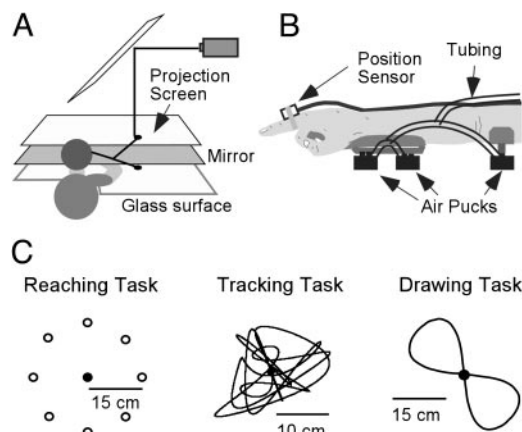


FIG. 1. Experimental apparatus and motor tasks. *A*: participants made movements on a horizontal glass surface while viewing the reflected image of visual feedback projected onto a rear projection screen in a semisilvered mirror. *B*: the arm was supported by lightweight air sleds to allow near-frictionless motion of the arm over the glass surface. *C*: participants made out and back movements to one of eight radial targets from a central starting point in the reaching task. The tracking task required participants to track a moving target with their hand cursor. Pattern shown is movement path of the target. In the drawing task, participants were presented with figure-eight templates in four possible orientations (0° , 45° , 90° , 135°) and asked to duplicate the figure using their hand cursor.

Tasks

REACHING TASK. Participants made out-and-back reaching movements on the horizontal work surface from a center start target (radius = 1 cm) to one of eight radial targets (radius = 0.75 cm) located 15 cm from the start position at angles ranging from 0° to 315° in 45° increments (Fig. 1C). Participants were asked to move out and back in a “fast and smooth motion” and to avoid corrective adjustments if they missed the target. The start location was positioned in the participants’ midsagittal plane such that the elbow was flexed at 90° when the hand was placed at that point. Participants were shown a cursor (radius = 0.75 cm) to indicate hand position during the task. This visual feedback was rotated about the start position to achieve different degrees of visuomotor rotation. Targets were presented sequentially from 0° to 315° forming a cycle. Each session consisted of 240 trials or 30 cycles of 8 trials.

TRACKING TASK. In this task, participants tracked a moving target with their hand cursor on the horizontal work surface. Both the target and hand cursor were 0.75 cm in radius. The trajectory of the target was determined using a sum of 5 sine-wave functions of different frequencies (0.36, 0.45, 0.63, 0.81, 0.90 Hz). This composite function created a smooth motion that was sufficiently unpredictable to discourage memorization of the target trajectory (Fig. 1C). The velocity of the target varied continuously between 1.2 and 104 cm/s with a mean of 44.7 cm/s and SD of 22.0 cm/s. The start position of each trial was determined in a similar manner as in the reaching task. Each session consisted of 16 trials of 35 s each. Visual feedback of hand position was rotated about the start position to produce a visuomotor rotation. Subjects were instructed simply to track the target as closely as possible.

DRAWING TASK. In each trial, a figure-eight template in one of four orientations (0° , 45° , 90° , 135°) was presented 25 cm in front of the participants together with a red circle that indicated the starting position for the movement. Participants began each trial by positioning their hand cursor at this starting position and proceeded to copy the figure-eight template, which remained visible throughout the trial. They were encouraged to draw the figure-eight in “one fast and smooth motion” and to avoid any deliberate corrective adjustments. The orientation of the templates progressed sequentially from 0° to

135° over trials. Each session consisted of 120 trials or 30 cycles of 4 trials from 0° to 135°.

Procedure

Visuomotor rotations of +30° and -30° were used in different conditions for this study. In each case, the hand cursor presented to the participants was rotated around the start position in each task. For example, participants who performed the reaching task under a +30° visuomotor rotation were shown a hand cursor that was rotated 30° counterclockwise from the true hand position. To compensate for the transformation, these participants had to make movements directed 30° clockwise from their natural movements.

Participants in groups 1, 2, and 3 all performed 30 cycles of the reaching task under a +30° visuomotor rotation on successive days (day 1 and day 2). Five minutes after completing the reaching task under the +30° rotation on day 1, participants in all three groups then experienced a -30° rotation. However, each group experienced this opposite rotation in a different task with groups 1, 2, and 3 performing 30 cycles in the reaching, tracking, and drawing tasks, respectively. During the 5 min between tasks, subjects remained in the apparatus and rested. Although they were not explicitly instructed to remain immobile, we did not observe any subjects making many arm movements during the break. Participants in group 4 also performed 30 cycles of the reaching tasks under the +30° rotation on successive days. However, these participants did not experience a second, opposite rotation on day 1. Thus group 4 served as a control that enabled us to evaluate possible retrograde interference effects attributed to experiencing the -30° rotation, in the different tasks, after the +30° rotation on day 1.

Groups 5 and 6 were included as controls to assess potential anterograde interference effects in groups 2 and 3, respectively, and to confirm that participants could retain learning of visuomotor rotations experienced in the tracking and drawing tasks. Participants in group 5 experienced the -30° rotation in the tracking task and were retested 24 h later under the same conditions. Participants in group 6 also experienced the -30° rotation on successive days but did so while performing the drawing task. Group 8 experienced the -30° rotation in the reaching task and served as control subjects to assess anterograde interference in group 1 who completed the -30° rotation 5 min after the +30° rotation. Finally, group 7 participants were exposed to the tracking task without a visuomotor rotation and served as controls to assess the extent to which adaptation in this task involved learning tracking per se.

Data analysis

The x and y hand position data were digitally smoothed using a fourth-order, low-pass Butterworth filter with a cutoff frequency of 12 Hz. To obtain measures of performance in the reaching task, we first differentiated the position signals with respect to time to obtain velocities using a three-point central difference equation. The tangential velocity of the hand was then computed as the resultant of the x and y velocities. Movement onset was set as the time at which the tangential velocity first exceeded 2 cm/s. The direction error at the first velocity peak or 150 ms after movement onset, whichever came first, was used as the measure of performance for the reaching task. This error was the difference between the vector from the start position to the hand position and the vector from the start position to the desired target at that instant.

A different measure of direction error was used to assess performance in the drawing task. First, we computed the time-varying displacement of the hand from the start position as the resultant of the x and y displacements. Each trial yielded two clear peaks in resultant displacement that corresponded to the two turnaround points of the figure-eight where the hand was maximally displaced from the origin. We took the hand positions at these displacement peaks and computed

the directions of the two vectors that joined each of these points to the start position. We defined the orientation of the figure-eight as the average of these two directions (first adding 180° to one of the directions so that they did not cancel one another). The difference between the orientation of the drawn figure-eight and that of the presented template gave the measure of direction error for the drawing task.

Finally, performance in the tracking task was assessed using the root-mean-square distance between the position of the moving target and the hand cursor (i.e., root-mean-square error). The first 5 s of each trial were discarded to allow time for participants to react to the onset of target movement. The remaining 30 s of the trial were sectioned into 3 epochs of 10 s each and the root-mean-square error was computed for each epoch. A trial mean was then determined as the average of these epoch errors.

In assessing the retention of learning and potential interference effects, we focused on the initial performance in a given experimental session. For the reaching and drawing tasks, we first computed, for each subject, the mean directional error for each cycle (averaging across the 8 or 4 trials per cycle, respectively), then took the average of the second and third cycles (see Krakauer et al. 1999; Tong et al. 2002) to quantify performance. In the tracking task, we used the root-mean-square in the first trial. Between- and within-subject analyses of variance (ANOVAs) were used to test various experimental effects using a significance level of 0.05.

RESULTS

Cursor paths produced by a single participant under the +30° visuomotor rotation for the first and last (30th) cycles are shown in Fig. 2A and Fig. 2B, respectively. Although initial directional errors were observed in the first cycle (Fig. 2A), directional errors were reduced close to zero by the last cycle (Fig. 2B). Figure 2D shows the directional error for each of the 240 trials under the +30° rotation for the same participant. These directional errors were taken at the first velocity peak or 150 ms after movement onset in each trial, whichever came first. In most trials, the initial velocity peak occurred just within the 150-ms epoch after movement onset, as shown in the sample tangential velocity profile of the hand in Fig. 2C.

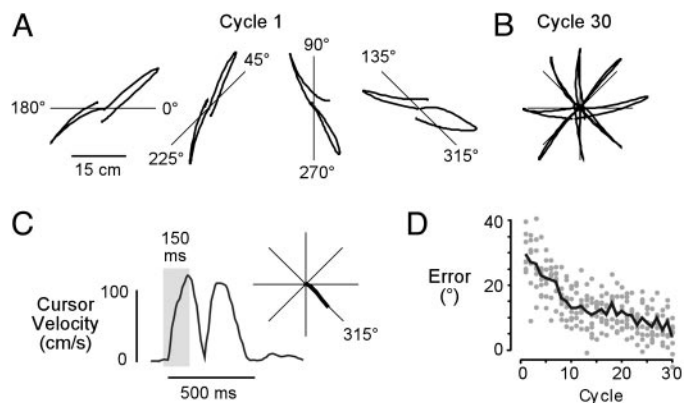


FIG. 2. Cursor paths and directional errors from single trials. *A*: cursor paths from the first eight movements (cycle 1) under the +30° rotation in the reaching task. For clarity, two movement paths (directed to opposing targets) are shown in each plot. *B*: cursor paths for the last eight movements (trials 232–240, cycle 30). *C*: tangential velocity profile of the hand for the last movement to the 315° target. The gray bar is aligned at movement onset and is 150 ms wide. *D*: angular direction errors for a single subject in 30 cycles of the reaching task under the +30° rotation.

Learning in control groups

Before testing for possible interference effects among the three tasks we examined, it was necessary for us to demonstrate that participants could learn the visuomotor rotation in each of these tasks as indicated by an improvement of performance across successive days.

Figure 3A shows learning curves for participants in group 4 who encountered the $+30^\circ$ visuomotor rotation while performing the reaching task on days 1 and 2. On day 1 (solid curve), the initial angular error was approximately 30° and matched the amplitude of the rotation. The angular error decreased gradually over about 20 cycles and reached a plateau of about 10° . On day 2 (dashed curve), the initial angular error was smaller and a similar plateau was reached within about 10 cycles. Plateaus of similar amplitude have been observed in several previous studies in which different arm configurations and visual displays were used (Krakauer et al. 1999; Tong et al. 2002; Wigmore et al. 2002). To quantify learning across days, we computed the average error across the second and third cycles of each task as an index of initial performance and then compared initial performances on day 1 and day 2. Participants in group 4 (Fig. 3A) showed a significant improvement in initial performance [$F(1,7) = 27.69$; $P < 0.05$] from day 1 ($M = 25.07^\circ$, $SD = 1.93^\circ$) to day 2 ($M = 12.27^\circ$, $SD = 5.99^\circ$).

Figure 3B shows the learning curves for group 5 who were exposed to the -30° rotation while performing the tracking task on both days. On day 1, the tracking error gradually decreased from about 15 cm to about 10 cm across the 15 trials (solid curve). On day 2, the tracking error was relatively constant and under 10 cm throughout the session (long dashed curve). The initial performance on each day was quantified using the average tracking error in the first trial. Significant retention of learning [$F(1,7) = 174.1$; $P < 0.001$] was observed with a clear reduction in error from day 1 ($M = 15.53$ cm, $SD = 2.17$ cm) to day 2 ($M = 7.97$ cm, $SD = 1.54$ cm). When adapting to the tracking task, subjects were presumably learning both the visuomotor rotation as well as the task per se. To demonstrate that the visuomotor rotation formed a significant aspect of this learning, we ran an additional group of subjects who experienced the tracking task without a visuomotor rotation (group 7). The short-dashed curve in Fig. 3B shows the learning curve for this group. The initial performance in this group was significantly better than the day 1 performance of group 5 who were exposed to the visuomotor rotation [$F(1,13) = 25.5$; $P < 0.001$]. However, there was no reliable difference between these two groups by trial 15 [$F(1,13) = 0.02$; $P = 0.89$]. These results indicate both that the initial performance of group 5 was impaired by the visuomotor rota-

tion and that the participants in this group adapted to the rotation.

Figure 3C shows learning curves for participants in group 6 who experienced the -30° rotation during the drawing task on days 1 and 2. In this case, the initial angular error on day 1 was approximately -25° . Over the 30 cycles, the magnitude of the error decreased, rapidly at first and then more gradually, to close to 0° . On day 2, the magnitude of the initial error was considerably smaller and then quickly decreased—over a couple of cycles—toward 0° . Again, to quantify learning over days, we computed the average angular error of the second and third cycles and used this as a measure of initial performance on each day. A significant improvement in initial performance across days was observed [$F(1,7) = 14.40$; $P < 0.05$]. The initial angular error on day 2 ($M = -1.52^\circ$, $SD = 3.56^\circ$) was much smaller in magnitude than that on day 1 ($M = -15.34^\circ$, $SD = 9.69^\circ$).

The results described above indicate that learning of the visuomotor rotation was retained across days regardless of the task in which the participants experienced the rotation. All three control groups (group 4, group 5, and group 6) showed significant improvement in their performance from day 1 to day 2.

Retrograde interference

The main goal of this investigation was to examine the possible interference effects between opposing visuomotor rotations experienced in different tasks. Groups 1, 2, and 3 all experienced the $+30^\circ$ rotation during the reaching task on day 1 and were retested on the $+30^\circ$ rotation during the same reaching task on day 2. All three groups also experienced the -30° rotation on day 1, 5 min after having adapted to the $+30^\circ$ rotation. However, the three groups differed in terms of the task they performed under the -30° rotation. Groups 1, 2, and 3 experienced the -30° rotation while performing the reaching, tracking, and drawing tasks, respectively.

The learning curves in each of the three panels of Fig. 4A–C show angular errors on the reaching task under the $+30^\circ$ rotation for days 1 (solid curves) and 2 (dashed curves). Figure 4A shows the learning curves for participants in group 1 who were successively exposed to opposite visuomotor rotations under the same reaching task on day 1. The fact that the learning curves for days 1 and 2 are very similar suggests that these participants did not retain learning across days. This finding replicates the results reported by Krakauer et al. (1999) and Wigmore et al. (2002). In contrast, as indicated by the curves shown in Fig. 4, B and C, participants in groups 2 and 3 appeared to retain much of what they learned on day 1 when

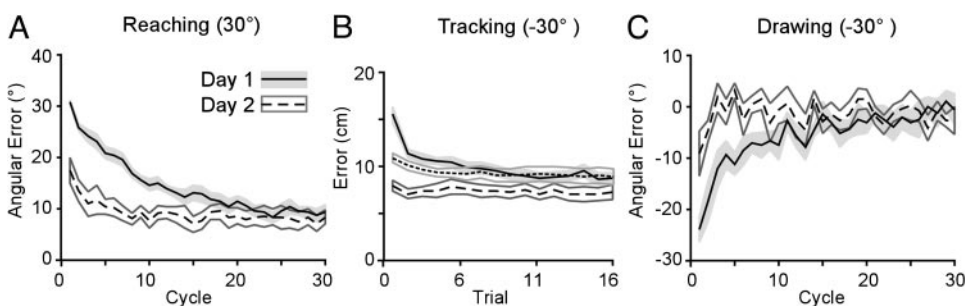


FIG. 3. Adaptation and retention of learning for visuomotor rotations in three different tasks. A and C: mean angular error as a function of cycle in the reaching and drawing tasks, respectively. B: mean distance error as a function of trial. Solid and dashed curves show performance on day 1 and day 2, respectively. Additional short-dashed curve in B shows performance of a naive control group on the tracking task without visuomotor rotation. Height of region associated with each curve represents ± 1 SE.

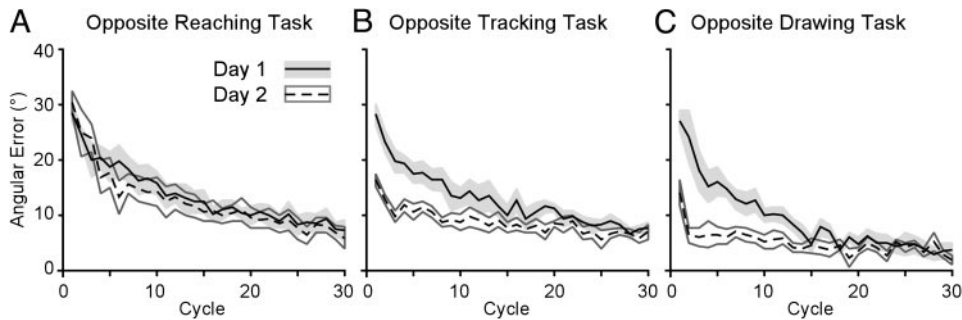


FIG. 4. Learning curves illustrating potential retrograde interference effects between successively learned opposing rotations. Each curve shows the mean angular error as a function of cycle in the reaching task under the $+30^\circ$ rotation. Solid and dashed curves indicate performance on days 1 and 2, respectively. Retrograde interference was seen in participants who experienced the opposing rotation in the same reaching task on day 1 (A) but not in participants who experienced the opposing rotation in the tracking (B) or drawing task (C). Height of region associated with each curve represents \pm SE.

retested on day 2. Thus exposure to the -30° rotation under the tracking (group 2) or drawing (group 3) tasks did not completely interfere with the learning of the $+30^\circ$ rotation, acquired immediately before, in the reaching task.

To quantify these interference and retention effects, we computed the average angular error over the second and third cycles of the reaching tasks as a measure of initial performance on each day. For group 1 (Fig. 4A), complete retrograde interference was observed in that the initial performances on day 1 ($M = 22.26^\circ$, $SD = 5.75^\circ$) and day 2 ($M = 24.40^\circ$, $SD = 8.67^\circ$) were not significantly different [$F(1,7) = 1.68$; $P = 0.24$]. In contrast, reliable differences in initial performance across days were observed for group 2 [$F(1,7) = 31.98$; $P = 0.001$] and group 3 [$F(1,7) = 24.47$; $P = 0.002$]. Although these results indicate that participants in groups 2 and 3 improved across days, the question remains as to whether this improvement was as great as in participants in group 4 (Fig. 3A) who experienced the $+30^\circ$ rotation only under the reaching task on day 1. To address this issue, we assessed interactions between group and day when including either groups 2 and 4 or groups 3 and 4. When considering only groups 2 and 4, there was no significant interaction between day and group [$F(1,14) = 0.71$; $P = 0.42$]. Similarly, there was no interaction between day and group [$F(1,14) = 0.30$; $P = 0.59$] when considering groups 3 and 4. Thus exposure to the opposite rotation in a different task did not result in any added interference beyond that observed for simply waiting a day.

To summarize, complete retrograde interference was observed when participants adapted to opposite rotations using

the same task. However, when the $+30^\circ$ and -30° rotations were learned during different tasks, no interference was observed and participants exhibited retention of learning similar to that of a control group exposed only to the $+30^\circ$ rotation on both days.

Anterograde interference

In addition to retrograde effects, we also assessed potential anterograde interference that may occur when participants are exposed successively to two visuomotor rotations that are equal and opposite. Figure 5A shows the learning curves for the reaching task under the -30° rotation for group 1, who had adapted to the $+30^\circ$ rotation in the reaching task 5 min earlier (dashed curve). The initial performance under the -30° rotation ($M = -37.4^\circ$) was significantly worse [$F(1,12) = 20.3$; $P < 0.01$] than that of naive control subjects (group 8) who experienced the -30° rotation in the reaching task without prior exposure to the $+30^\circ$ rotation (solid curve; $M = -13.9^\circ$). Thus as expected from previous work (Wigmore et al. 2002), clear anterograde interference was observed when successively adapting to opposing rotations within the same reaching task.

The question of interest in the current study is whether such anterograde interference effects are observed across changes in task. Figure 5B shows learning curves for the tracking task under the -30° rotation for group 2, who had adapted to the $+30^\circ$ rotation in the reaching task 5 min earlier (dashed curve), and group 5, who did not (solid curve). As is evident in the figure, previous adaptation to the $+30^\circ$ rotation did not result

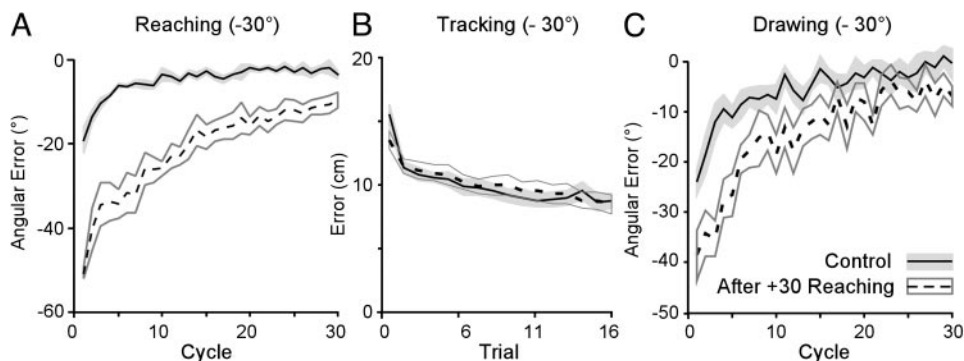


FIG. 5. Learning curves illustrating potential anterograde interference effects between successively experienced opposing rotations. A: mean angular error as a function of cycle in the reaching task under the -30° rotation. Solid and dashed curves show performance for naive subjects and subjects who previously experienced the $+30^\circ$ rotation in the reaching task, respectively. B: mean distance errors in the tracking task as a function of trial under the -30° rotation. Solid and dashed curves show performance in naive subjects and subjects who were previously exposed to the $+30^\circ$ rotation in the reaching task. C: mean angular error in the drawing task as a function of cycle under the -30° rotation. Solid and dashed curves show performance for naive subjects and subjects who previously experienced the $+30^\circ$ rotation in the reaching task. Height of region associated with each curve represents ± 1 SE.

in increased tracking error. ANOVA based on errors in the first trials revealed that there was no reliable difference in initial performance errors between the two groups [$F(1,14) = 3.98$; $P > 0.07$]. Thus clear anterograde interference was not observed from the reaching task to the tracking task.

Figure 5C shows learning curves for the drawing task under the -30° rotation for group 3, who had previously adapted to the opposite rotation in the reaching task (dashed line), and group 6, who had not previously adapted to any rotation. In contrast to the results for the tracking task, here we observed clear anterograde interference. Analysis of initial performance based on average errors in the second and third cycles, yielded a significant difference between the two groups [$F(1,14) = 24.71$; $P < 0.05$]. The initial errors for group 3 ($M = -34.71^\circ$, $SD = 6.73^\circ$) were notably greater than the errors for group 6 ($M = -18.33^\circ$, $SD = 6.45^\circ$). Thus anterograde interference was observed from the reaching task to the drawing task.

DISCUSSION

Several studies have shown that when people successively adapt to opposing visuomotor (Krakauer et al. 1999; Wigmore et al. 2002) or dynamic (Brashers-Krug et al. 1996) transformations without changing the task or context, learning of the first is not consolidated in memory. This retrograde interference is believed to result from competition for resources in short-term or working motor memory such that learning the second transformation overwrites memory of the first (Brashers-Krug et al. 1996; Krakauer et al. 1999; Shadmehr et al. 1997). Although it is also possible that retrograde interference may reflect a failure of recall rather than consolidation, arguments against this interpretation have been put forward by Shadmehr and Brashers-Krug (1997). The goal of the present study was to determine whether the retrograde interference observed when learning opposing transformations can be eliminated or attenuated if the two transformations are encountered during different tasks. If so, it would suggest that distinct resources in motor working memory could be allocated to learning opposing transformations experienced in different tasks.

We found that participants who successively adapted to opposite visuomotor rotations while performing different tasks showed full retention of the first rotation when retested a day later. Their performance on day 2 did not differ from that of participants who were exposed only to the first rotation on days 1 and 2. In contrast, participants who encountered the opposite rotations consecutively in the same reaching task showed no retention for the first rotation on day 2, replicating the complete retrograde interference shown in previous literature (Krakauer et al. 1999; Wigmore et al. 2002).

These results suggest that when subjects adapted to opposing visuomotor rotations, experienced in different tasks, they acquired distinct, task-specific internal models or representations of these rotations that were independently consolidated in long-term memory. This finding would appear contrary to the results of Conditt and colleagues (1997). These authors demonstrated that learning of a novel rotary viscous force field generalizes across different tasks. This indicates that subjects acquired an internal model of the force field and were able to apply the same internal model under different task conditions. In other words, they did not acquire a task-specific internal

model of the force field. Although the results of the present study and those of Conditt et al. (1997) appear to be inconsistent, there are a number of differences between the two studies that may account for this apparent discrepancy.

Whereas Conditt and colleagues (1997) examined the learning of a dynamic perturbation that altered the mapping between force and resulting motion, we investigated learning of kinematic transformations that altered visual feedback. Krakauer and colleagues (1999) recently argued that separate working memory systems are used when learning internal models for kinematic and dynamic transformations. Thus it is possible that the difference between our results and those of Conditt reflect differences in the organization of kinematic and dynamic working memory systems. However, a recent study by Tong et al. (2002) showed interference between kinematic and dynamic learning, thereby challenging the idea that kinematics and dynamics are learned using distinct working memory systems. Instead, the Tong et al. (2002) results suggest that internal models for novel kinematic and dynamic perturbations may share common resources.

Another factor that may have contributed to the discrepancy between our results and those of Conditt et al. (1997) pertains to the state spaces explored by the different tasks. Conditt and colleagues used a velocity-dependent force field where the magnitude and direction of the perturbing force depended on both the magnitude and direction of velocity. In the different tasks used in their study, subjects experienced similar ranges of velocity magnitudes and directions. Thus in all tasks, the mapping between states and forces—defined by the force field—was similar. This similarity was likely an important factor contributing to the strong transfer of learning across tasks. Had the states experienced in the two tasks been different, some degradation in performance might be expected (e.g., Gandolfo et al. 1996; Krakauer et al. 2001). The question arises as to whether the independence between tasks, observed in the present study, can be explained in terms of differences in the state spaces associated with our tasks. The visuomotor rotations used in our experiment were position-dependent transformations with the size and direction of the perturbation (displacement of viewed hand position) dependent on the position of the hand relative to the origin (starting hand position in all tasks). In our three tasks, movements were carried out in similar regions of space (see Fig. 1C). In particular, all three tasks involved hand positions in all directions from the origin and of similar extent. Thus in general, subjects experienced a similar range of hand positions—and hence similar visual perturbations—in all three tasks. To compare hand velocities across the three tasks, we carried out an additional analysis focusing on those subjects who performed both the reaching and tracking tasks (group 2) or both the reaching and drawing tasks (group 3). In both cases, we compared hand velocities in the reaching task with hand velocities in the nonreaching task (both performed on day 1). We computed the peak velocity for each trial and subject and then carried out repeated-measures ANOVAs based on subject means. We found no significant difference in peak velocities between the reaching and tracking tasks [$F(1,7) = 1.67$; $P > 0.05$] but did observe that peak velocity in the reaching task ($M = 1.46$ m/s) was reliably greater [$F(1,7) = 15.6$; $P < 0.01$] than in the drawing task ($M = 1.32$ m/s). Although we cannot claim that our tasks were perfectly matched in terms of state space, there was undoubt-

edly considerable overlap. As a consequence, if interference were state-space dependent, we would expect at least some interference between tasks. However, we found complete independence when the opposite rotations were learned during the different tasks. It therefore seems unlikely that the independence we observed can be explained in terms of differences in the state space visited in each task.

Our study and the study of Conditt et al. (1997) also differ in terms of the experiment paradigms employed. Whereas Conditt and colleagues examined anterograde facilitation—how learning from one task transfers to a second task, we focused on retrograde interference—how new learning in one task affects the retention of previous learning in a different task. A key question is whether anterograde facilitation across two tasks can occur even if there is no retrograde interference when opposing transformations are learned successively in the same pair of tasks. If so, the results of the two studies, related to task effects, are not necessarily inconsistent. Evidence that anterograde effects can occur without retrograde effects comes from the present study. We observed clear anterograde interference from the reaching task to the drawing task. Subjects who first experienced the $+30^\circ$ rotation in the reaching task subsequently performed worse on the -30° rotation in the drawing task than control subjects who performed only the latter task. However, we found no evidence of retrograde interference between the same two tasks. Subjects who experienced the $+30^\circ$ rotation in the reaching task, followed immediately by the -30° rotation in the drawing task, showed full retention of the $+30^\circ$ rotation when retested the next day. Their performance on the second day equaled that of control subjects who experienced only the $+30^\circ$ rotation on the first day. Thus we observed anterograde interference from the reaching task to the drawing task without any retrograde interference from the drawing task to the reaching task.

So how do we explain this result? As noted above, it has been suggested that learning a novel sensorimotor transformation involves two steps: initial acquisition of an internal model in short-term memory followed by gradual consolidation of an internal model in long-term memory (Brashers-Krug et al. 1996). Within this framework, one can imagine a scenario in which anterograde interference between two (opposing) transformations can occur even though two distinct internal models will ultimately be consolidated into long-term memory. Suppose the participants exposed to a $+30^\circ$ visuomotor rotation in the reaching task acquire an internal model, IM1, in working memory. Five minutes later, the same participants are exposed to the opposite -30° rotation in the drawing task. The change in task provides contextual cues that trigger the allocation of separate working memory resources for a new internal model, IM2, but because IM1 was the last applied model, its contents are copied into this new memory space as a starting point for adaptation. Because IM1 compensates for a $+30^\circ$ rotation, we observe anterograde interference even though a distinct memory resource is being used in the second task to allow independent consolidation of internal models for both tasks.

An alternative explanation for our finding that anterograde interference can occur without retrograde interference may have to do with asymmetrical transfer of learning between tasks. Specifically, it may be that learning in the reaching task transfers (either positively or negatively) to the drawing task but not vice versa. One possibility is that such asymmetry arose

because the internal model learned during the drawing task was incomplete. However, this seems rather unlikely. Even if learning of the drawing task was incomplete, there was clearly substantial learning and therefore we would expect some amount of (retrograde) interference back to the reaching task on day 2. Our data, however, showed no evidence of any retrograde interference—performance on day 2 on the reaching task was not significantly different from that of control subjects who performed only the reaching task on days 1 and 2. How else can we explain this possible asymmetry? One idea is that when participants adapted to the drawing task, they started with the internal model previously adapted for the reaching task but learned a new internal model. The gradual learning in the drawing task could reflect the development of this new model operating in parallel with the previous (but unchanged) internal model, both of which are subsequently consolidated into long-term motor memory.

Having discussed the lack of retrograde interference in some detail, let us now consider the pattern of anterograde effects observed among our 3 tasks. We observed anterograde interference from the $+30^\circ$ rotation in the reaching task to the opposite -30° rotation in the drawing task, but not from the $+30^\circ$ rotation in the reaching task to the -30° rotation in the tracking task. This suggests that what was learned during adaptation to a visuomotor rotation depended on the task in which the transformation was experienced. Specifically, when adapting to a visuomotor rotation under the tracking task, subjects may have represented the transformation differently than when adapting to the same transformation under the reaching or drawing tasks. Thus the independence we observed between the tracking and reaching tasks, in particular, may be attributed to the fact that different internal models were developed to perform these two tasks. When people adapt to a particular transformation, they do not necessarily acquire an accurate internal model of the transformation. For example, when subjects adapt to a visuomotor rotation in a center-out reaching task in which they are required to “touch” the target in each trial, they may quite quickly learn to aim the hand in the direction of the target but still experience difficulties making corrective adjustments when they miss the target (unpublished observations). In other words, subjects may learn only those components of a transformation needed to perform a particular task without learning the full transformation (see, for example, Krakauer et al. 2001).

In summary, we found strong evidence for the development of task-specific internal models for visuomotor rotations. Independent consolidation of internal models for opposite visuomotor rotations was observed when they were presented in different task conditions. Task changes may allow opposing transformations—that normally interfere with one another—to be learned independently by providing strong contextual cues or by altering the way in which the transformations are represented.

DISCLOSURES

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REFERENCES

Blakemore SJ, Wolpert DM, and Frith CD. Central cancellation of self-produced tickle sensation. *Nat Neurosci* 1: 635–640, 1998.

- Bock O, Schneider S, and Bloomberg J.** Conditions for interference versus facilitation during sequential sensorimotor adaptation. *Exp Brain Res* 138: 359–365, 2001.
- Brashers-Krug T, Shadmehr R, and Bizzi E.** Consolidation in human motor memory. *Nature* 382: 252–255, 1996.
- Condit MA, Gandolfo F, and Mussa-Ivaldi FA.** The motor system does not learn the dynamics of the arm by rote memorization of past experience. *J Neurophysiol* 78: 554–560, 1997.
- Cunningham HA and Welch RB.** Multiple concurrent visual-motor mappings: implications for models of adaptation. *J Exp Psychol Hum Percept Perform* 20: 987–999, 1994.
- Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, and Kawato M.** Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. *J Neurosci* 19: RC 34: 1–5, 1999.
- Flanagan JR and Wing AM.** The role of internal models in motor planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17: 1519–1528, 1997.
- Gandolfo F, Mussa-Ivaldi FA, and Bizzi E.** Motor learning by field approximation. *Proc Natl Acad Sci USA* 93: 3843–3846, 1996.
- Goodbody SJ and Wolpert DM.** Temporal and amplitude generalization in motor learning. *J Neurophysiol* 79: 1825–1838, 1998.
- Johansson RS and Cole KJ.** Sensory-motor coordination during grasping and manipulative actions. *Curr Opin Neurobiol* 2: 815–823, 1992.
- Kawato M.** Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–727, 1999.
- Krakauer JW, Ghilardi MF, and Ghez C.** Independent learning of internal models for kinematic and dynamic control of reaching. *Nat Neurosci* 2: 1026–1031, 1999.
- Krakauer JW, Pine ZM, Ghilardi, M-F, and Ghez C.** Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000.
- Lackner JR and DiZio P.** Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72: 299–313, 1994.
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, and Thach WT.** Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119: 1199–1211, 1996.
- Miall RC, Weir DJ, Wolpert DM, and Stein JF.** Is the cerebellum a Smith predictor? *J Motor Behav* 25: 203–216, 1993.
- Muellbacher W, Ziemann U, Wissel J, Dang N, Kofler M, Facchini S, Boroojerdi B, Poewe W, and Hallett M.** Early consolidation in human primary motor cortex. *Nature* 415: 640–644, 2002.
- Seidler RD, Bloomberg JJ, and Stelmach GE.** Context-dependent arm pointing adaptation. *Behav Brain Res* 119: 155–166, 2001.
- Shadmehr R and Brashers-Krug T.** Functional stages in the formation of human long-term motor memory. *J Neurosci* 17: 409–419, 1997.
- Shadmehr R and Mussa-Ivaldi FA.** Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.
- Vetter P, Goodbody SJ, and Wolpert DM.** Evidence for an eye-centred spherical representation of the visuomotor map. *J Neurophysiol* 81: 935–939, 1999.
- Wigmore V, Tong C, and Flanagan JR.** Visuomotor rotations of varying size and direction compete for a single internal model in motor working memory. *J Exp Psychol Hum Percept Perform* 28: 447–457, 2002.
- Wolpert DM and Ghahramani Z.** Computational principles of movement neuroscience. *Nat Neurosci* 3: 1212–1217, 2000.
- Wolpert DM, Ghahramani Z, and Jordan MI.** An internal model for sensorimotor integration. *Science* 269: 1880–1882, 1995.