# Consolidation in Human Motor Learning

by

Thomas M. Brashers-Krug

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## Abstract

The experiments presented in this thesis were conducted to probe motor memory for its component processes. Subjects learned to move a two-link planar manipulandum to a series of targets. The manipulandum perturbed their movements first with one and then with a second, opposite pattern of velocity-dependent forces. In Experiment 1, subjects were impaired in their ability to learn to control the manipulandum in the second pattern of forces when the second pattern was presented within 5 minutes of the first. This phenomenon is known as negative transfer (NT). In Experiment 2, a second group of subjects retained their ability to perform in one pattern of forces after a 24 hour break. There was no NT, however, when a third group of subjects waited 24 hours between learning the two different patterns of forces. These experiments showed that learning a new motor skill can cause two distinct and specific effects with separate time courses: transient NT and a lasting improvement in skill.

Learning can set in motion neural processes that continue to evolve for a period of time after practice on a task has ended [9, 33, 39, 67, 71]. This phenomenon is known as consolidation [39, 67, 71]. The experiments in Chapter 2 explored the consolidation of motor learning. Subjects learned to control the manipulandum while it perturbed their movements with one pattern of forces. They then learned to guide the manipulandum while it produced a second pattern of forces, either immediately after the first pattern or after a break of either 4 or 8 hours. When subjects learned the two different patterns of forces one immediately after the other, they experienced a mutual interference between the tasks: performance in the second task was reduced in all subjects, and 24-hour retention of the first task was virtually eliminated. By contrast, subjects who waited either 4 or 8 hours between learning the first and second patterns showed significantly less interference. The motor memory had consolidated within 4 to 8 hours. The disruption of consolidation through specific behavioral interventions has previously been shown to occur in explicit memory, which depends on different neural structures than motor memory [44, 15]. The results in this thesis suggest that distinct neural systems share similar characteristics when encoding and storing new information.

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# Chapter 1

# Introduction

The experiments presented in this thesis were conducted to probe motor memory for its component processes. Learning and memory have typically been divided into two categories. These two distinct types of memory have been described variously as explicit and implicit [54, 55], declarative and nondeclarative [64], and memory with awareness and memory without awareness [29]. According to Schacter [54], explicit memory involves the conscious recollection of events or facts, while implicit memory is not consciously available and so must be measured by its effect on performance. The retention of motor learning is one type of implicit memory. Explicit memory has frequently been divided into component processes or states, while motor memory has not been comparably divided. In models of explicit memory, these processes or states can exist either in sequence or in parallel. One example of the former type of model in which two states of memory exist in sequence can be found in the "modal model" of memory proposed by Atkinson and Shiffrin [6]. In that model, memories are shifted from an initial short-term storage to a more permanent long-term storage. An example of the latter type of model, in which the component parts of explicit memory exist in parallel, is the working memory model of Baddeley [7]. In Baddeley's model, a supervisory control system, the central executive, regulates two subsidiary parallel processes, the visuo-spatial sketchpad and the phonological loop.

There was a period of investigation several decades ago into what was called short-term motor memory [2, 50]. Those experiments, however, did not claim that the short-term motor memories were ever transformed into long-term motor memories. Their results thus indicated that one type of motor memory could be fleeting, not that motor memories contained distinct, sequential components. The experiments in Chapter 1 show that learning a new motor skill can cause two distinct and specific effects with separate time courses: a transient negative transfer (NT) and a lasting improvement in skill. This result indicates that motor memory is not a unitary phenomenon. Two possible models can account for this finding. In the first, two parallel effects are created as a result of motor learning. The first effect is a lasting skill in the practiced task. The retention of this skill is what is commonly referred to as motor memory. The second effect is a transient NT. NT decreases with time, disappearing within 24 hours. In this model, both effects are created when learning occurs. One endures, whereas the other does not. The second possible model is a consolidation model [39, 67, 71]. The motor memory is transformed with time from a state in which it causes NT to one in which it does not cause NT. In this model, the way the motor learning is stored changes with the passage of time. This is a sequential model, with the two stages of motor memory occuring one after the other. The nature of the change from one stage of motor memory to the other is not revealed by these experiments, but possibilities include a change in anatomical locus [74] or a change in the biochemical substrate in which the learning is embedded [9, 67].

The experiments in Chapter 2 were conducted to distinguish between these two models. The results presented in Chapter 2 suggest that the consolidation model is the more likely of the two. Those results provide the first demonstration that the consolidation of human motor memory can be disrupted through behavioral means in a time-dependent manner. When first formed, motor memories can be disrupted by a second motor learning task. This is no longer the case if 4 to 8 hours elapse before the second task is learned.

Together, the results in Chapters 1 and 2 suggest that motor memory can be transformed over time and in the absence of practice. Motor memory first exists in an initial state in which it affects the ability to learn a second task and is vulnerable to being disrupted by the second task. From this initial, transient state the motor memory can become consolidated into a form in which it neither interferes with nor is affected by learning a second motor task. The disruption of consolidation through specific behavioral interventions has been shown to occur in explicit memory, which depends on different neural structures than motor memory [44, 15]. By extending the phenomenon of consolidation to motor memory, these results suggest that distinct neural systems share similar characteristics when encoding and storing new information.

# Chapter 2

# Separable Effects of Motor Learning

## Abstract

**The experiments presented in this chapter were conducted to probe motor memory for its component processes. Right-handed subjects (n = 30; male/female: 12/18), 18-35 years old (mean ± SD: 21.9 ± 3.0), learned to move a two-link planar manipulandum to a series of targets with their right hands. The manipulandum perturbed their movements first with one and then with a second, opposite pattern of velocity-dependent forces. Each pattern of perturbations lasted approximately 5 minutes. In Experiment 1, subjects were impaired in their ability to learn to control the manipulandum in the second pattern of forces when the second pattern was presented within 5 minutes of the first. This phenomenon is known as negative transfer (NT). In Experiment 2, a second group of subjects retained their ability to perform in one pattern of forces after a 24 hour break. There was no NT, however, when a third group of subjects waited 24 hours between learning two different patterns of forces. Learning a new motor skill can cause two separate and specific effects with distinct time courses: transient NT and a lasting improvement in skill.**

**These separate effects of motor learning — retention of the task learned and NT — suggest either of two models of motor memory. In the first model, a newly formed motor memory is made up of at least two distinct components, one of which fades within 24 hours, and one of which endures for at least that long. In the second model, motor memory is transformed over time from its initial state to a later state with different properties. This latter model suggests a mechanism reminiscent of consolidation, where the substrate in which a memory is encoded changes over time.**

# Introduction

During the first half of this century there were many experimental studies of the ways in which learning one task affects the learning of a second task. One of the most influential researchers in this area, J. A. McGeoch, summarized decades of work on the subject in two chapters of his 1952 text, *The Psychology of Human Learning* [41]. Those studies showed that learning one task can make it easier or more difficult to learn a second task — positive or negative transfer (NT), respectively [35, 60, 73, 70, 14, 19, 24], — and learning a second task can facilitate or interfere with subsequent recall of a previously learned task — retrograde facilitation or retrograde interference (RI), respectively [26, 68, 21, 10, 42].

Studies of transfer and interference were dominated by an associationist interpretation [8]. Most reports analyzed their findings in terms of stimulus-response (S-R) associations [21, 14, 42]. An often-cited formalization of the S-R interpretation of transfer and interference was put forward by Charles Osgood [49]. Osgood fashioned a "surface of retroaction," with which he described the conditions under which learning two tasks would facilitate or interfere with each other. He concluded that the greatest degree of facilitation would occur when two tasks had similar stimuli and similar responses. Less facilitation would occur when two tasks had dissimilar stimuli and similar responses. Finally, two tasks would interfere with each other if they had similar stimuli but called for dissimilar responses.

The initial enthusiasm with which transfer and interference were pursued was dampened for two reasons. First, the phenomena themselves were wrapped up to such a strong degree with their S-R interpretation that their prominence as a focus of study faded with the fading of associationism in general. Second, once the theoretical explanation of transfer and interference had been laid out so clearly by Osgood and others, interest turned from an exploration of the conditions under which these effects occur to a search for their presence outside the rigid laboratory setting. McGeoch's optimism that interference could account for a large portion of forgetting in everyday life [41] was cut short by findings that contradicted the predictions of his explanations. McGeoch's response competition hypothesis proposed that forgetting could be explained in large part by the weakening of the S-R associations that were formed when learning occured. A second learning task would result in new S-R associations that would compete with the old associations at the time of recall. Response competition predicted that forgetting of the first task should be associated with intrusions, at the time of recall, from the second task. Melton and Irwin studied the phenomenon of intrusions in a task of verbal learning [43]. These authors concluded that overt intrusions could not account for many of the errors that occured when subjects learn two different lists of words. Although response competition provided only one explanation of how interference may cause forgetting, the predictive failure of the theory weakened interest in the phenomenon of interference in general.

Although interest in transfer and interference had dwindled [8] by the 1970s, three recent developments have made these phenomena relevant to modern research in learning and memory. First, the advent of cognitive neuroscience has initiated an exploration into the neural basis by which cognitive tasks are processed [20]. This development has opened new avenues of research in what had been a fairly narrowly defined field.

A second reason that transfer and interference are receiving renewed interest can be found in the growing recognition of learning-dependent plasticity in the nervous system [32]. This recognition has grounded the concepts of transfer and interference in the physical substrate of neural tissue and raised questions about how neural plasticity is organized to minimize unwanted interactions between one change and another. Third, the burgeoning neural network literature has provided a means for formalizing the study of transfer and interference, and has emphasized the difficulties that accompany coding and storing large amounts of sometimes contradictory information [31, 48, 18, 12].

Learning and memory have typically been divided into two categories: explicit and implicit [53]. Explicit memory involves the conscious recollection of events or facts. Implicit memory, on the other hand, is not consciously available and is often measured by its effect on performance. The majority of research on NT and RI has focused on tasks of explicit learning. There have been scattered reports of these phenomena in motor learning (one type of implicit learning), but the tasks used in these studies have always had a large explicit component (*e.g.*, recalling the direction of movement specified by a set of lights [34, 36] or by a number [59], or remembering a sequence of movements [58]). In fact, one study that claimed to report transfer in motor learning actually employed a task in which the supposedly motor component required that subjects learn to produce verbal responses to various visual stimuli [73].

The simple reaching task studied in the following series of experiments has little, if any, explicit component. One goal of the studies reported here was to determine the extent to which NT can occur in a predominately motor task. A second goal was to probe motor memory for its component parts. With the exception of an intense but short-lived period of research into what was called short term motor memory [2, 50], motor memory has been veiwed as a unitary phenomenon. The results of Experiment 2 suggest that this view ought to be reconsidered. The chapter is divided into two experimental sections. Experiment 1 examines negative transfer. Experiment 2 explores the effect of time on transfer and retention. An analysis of NT based on data from Experiments 1 and 2 is presented after Experiment 2. A brief discussion is included at the end of each experiment, and a comprehensive discussion at the end of the chapter.

# Experiment 1

## Method

### Subjects

Right-handed subjects (n = 10; male/female: 4/6), 18-35 years old (mean ± SD: 19.6 ± 1.6), recruited from the MIT community participated in this study. Subjects classified themselves as right-handed and reported that they did not have any neurological disorders. Subjects were paid for their participation. MIT's Committee on the Use of Humans as Experimental Subjects approved all experimental protocols.

### Apparatus

Subjects sat on a chair with an adjustable height. An adjustable sling suspended from the ceiling supported subjects' right arms in the horizontal plane. Subjects held the handle on one end of a two-link, planar manipulandum with their right hands (Fig. 2-1) [16]. Two torque motors (PMI Corp.) controled the two joints of the manipulandum. The torque motors delivered forces through the manipulandum to the subjects' hands. The forces were calculated as a function of the velocity of the hand in cartesian coordinates: $f = \mathbf{B}\dot{x}$. The matrix $\mathbf{B}$ was either $\begin{bmatrix} 0 & 13 \\ -13 & 0 \end{bmatrix} N \cdot sec/m$ or $\begin{bmatrix} 0 & -13 \\ 13 & 0 \end{bmatrix} N \cdot sec/m$. These matrices defined clockwise and counter-clockwise curl fields in velocity space, respectively (Fig. 2-3). Optical encoders and tachometers recorded the position and velocity, respectively, of the manipulandum's joints at 100 Hz. These data were transformed through a simple algorithm implemented in the software to provide the position and velocity of the handle at the end of the manipulandum.

A video display monitor, mounted above the base of the manipulandum, faced the subjects. A Gateway 2000 P5-66 computer controlled the manipulandum and the video display monitor.

## Procedure

In brief, subjects moved the handle of the manipulandum to a series of targets. After a period of initial, non-recorded practice, subjects were tested in 3 conditions over 2 days: baseline, Task A, and Task B. In the baseline condition, the manipulandum produced no forces. In Task A, the manipulandum perturbed subjects movements with one pattern of velocity dependent forces. The manipulandum then produced a pattern of forces in Task B that were opposite to those in Task A.

**Initial Practice** Subjects moved the handle of the manipulandum to guide a cursor to a series of targets that appeared one at a time on the computer monitor. The torque motors did not deliver any forces to the subjects' hands. The cursor started at the center of the monitor and remained visible on the screen throughout the session. Subjects moved the handle 10 cm to targets that appeared in one of eight directions: four directions starting from the center of the monitor (0°, 45°, 90°, 135°) and the four corresponding directions back to the center from each of those targets (180°, 225°, 270°, 315°; Fig. 2-2). A target set consisted of 192 targets and lasted approximately 5 minutes, the exact duration depending on each subject's movement times. Targets out from the center of the monitor were always followed by a target at the center. After the subject stopped the cursor at a target, that target disappeared and the next one appeared. The targets appeared in a pseudo-random order, constrained only in that subjects made a movement in each of the 8 directions 24 times during the target set.

Subjects were instructed to keep two goals in mind as they moved the handle from target to target. First, they were told that they should wait until a target appeared before starting a movement. Second, they were asked to move at a steady, experimenter-defined pace. To provide subjects with feedback on their movement times, the computer generated a short, distinctive buzzing sound if subjects reached the target within the goal of 500 ± 50 msec. Each movement was timed with a velocity threshold that indicated when subjects started that movement, not from the appearance of the target. A target turned blue if subjects reached it after 550 msec and red if they reached it before 450 msec. It took most subjects between 300 and 500 movements to master the task to a level at which they could reach most targets within the proper window of time.

**Baseline** When subjects were able to move consistently to the targets at the proper speed, 12 movements in each of the 8 target directions were recorded. These 96 movements comprised the subjects' baseline trajectories, against which later performance on Day 2 would be measured.

**Task A** On Day 2, subjects were allowed to refamiliarize themselves with the timing of the task by moving to approximately 50 targets in the absence of the perturbing forces before testing began. Immediately after this practice run, they were presented with the task of learning to move the manipulandum while it produced perturbing forces. The subjects' instructed goals were the same as during the baseline target session on Day 1. The subjects were told that the robot arm would push and pull their hands as they tried to move from target to target. Two torque motors delivered velocity-dependent forces to the handle of the manipulandum, perturbing the subjects' movements as they tried to guide it to the targets. For half the subjects, the perturbations during the first target set used clockwise forces, and for the other half, counterclockwise forces. Subjects practiced this task for one target set. This target set and pattern of forces will be refered to as Task A, regardless of the direction of the forces.

**Task B** After a 3-5 minute break, subjects were given a second target set. During this second target set, the pertubing forces were 180° opposite to the forces in the first target set. If a subject was perturbed with clockwise forces during the first target set, s/he was perturbed with counterclockwise forces during the second target set, and *vice versa.* This target set will be referred to as Task B, regardless of the direction of the forces during each set.

**Probe Targets** Eight of the targets out from the center intermixed throughout each set were presented without velocity-dependent forces and eight were presented with forces that were 180° opposite to the forces given in the other 176 movements. For example, if a subject's movements were perturbed by the clockwise forces for 176 movements in one target set, the forces would be turned off for 8 movements and counterclockwise forces would be applied for 8 movements spread throughout the target set. These targets will be referred to as null probe and 180° probe targets, respectively. These 16 targets were used to probe subjects' strategies in compensating for the forces (see Discussion section, and [57]). The forces that were present during the 176 targets that were neither null probe nor 180° probe targets will be called the learned forces.

## Measurements

**Correlation Coefficient** Learning was assessed using three measures of performance. First, a measure of correlation assigned a numerical value to the similarity between a subject's movements on Day 2 in the presence of the perturbing forces and his or her baseline movements on Day 1 (before the forces were turned on). This correlation measure revealed the extent to which a subject had adapted to the forces. The application of this measure has been validated in previous work, where it has been shown that, as a subject practices moving the handle of the manipulandum while it produces perturbing forces, his or her trajectories converge to those of the baseline [57]. The correlation coefficient captures this convergence.

The correlation coefficient, $\rho$, between two trajectories, $a$ and $b$, is the ratio of the covariance between $a$ and $b$ and the product of their standard deviations: $\rho(a,b) = \frac{\mathrm{Cov}(a,b)}{\sigma(a)\sigma(b)}$. $\rho$ can take a value from $-1$ to 1, with 1 indicating that two trajectories are identical, and -1 indicating that they move in 180° opposite directions.

**Movement Time and Path Length** The time from movement onset to movement termination was recorded as a second measure of performance. The movement time provided a measure of the subjects' ability to achieve the timing goal of the task. As a third measure, the path length of the subjects' movements was calculated by summing the velocity at each sampled instant along a trajectory and dividing this number by the sampling rate. Path length reflected the degree to which the forces perturbed, and thereby lengthened, the path subjects took as they moved to the targets. Note that these last two measures were combined in the measure of correlation, which gives an overall assessment of the subjects' trajectories.

### Criterion for Exclusion of Subjects

In order for the measure of correlation to reflect a subject's learning accurately, it was important that the subject try to replicate his or her movements from one session to the next. A small percentage of subjects disregarded the instructions to move at a steady pace from target to target. To identify these subjects objectively, the average peak velocity of a subject's trajectories in the baseline condition and in the various learning tasks was calculated. The ratio of the average peak velocity in the learning tasks to that of the baseline condition provided an indication of the amount by which a subject altered the speed of his or her trajectories from one condition to the next. Subjects whose ratios departed from the mean of all subjects' ratios by more than two standard deviations were excluded from further analysis. By this criterion, we excluded 2 of 30 subjects from our analysis in the two experiments. Both the excluded subjects were from the first experiment.

## Results

### Task A

When first exposed to the forces, subjects' movements deviated from the straight-line trajectories of the baseline (Fig. 2-4). After 5 minutes of practice, most subjects were able once again to move in a fairly straight line to the targets (Fig. 2-4). This improvement in their ability to control the manipulandum with practice resulted in a steady rise of the correlation coefficient (Fig. 2-5) of the movements during the learned forces. In addition, subjects' movement times approached the goal value of 0.5 sec., and their paths straightened out, as indicated by the convergence of the path lengths toward 10 cm.

By contrast, there was no improvement in the correlation coefficients of the trajectories to the 8 180° probe targets. The values of the correlation coefficients for the 4 180° probe targets in the first half of the target set were not significantly different from those in the second half of the target set ($0.68 \pm 0.05$ vs. $0.66 \pm 0.06$; $t(7) = 0.58$, $p = 0.58$)[1].

During the 8 null probe targets, when the viscous forces were turned off without warning, subjects' movements were rough mirror-images of their perturbed trajectories. These aftereffects have been observed previously in work with this motor learning paradigm [57].

### Task B

In order to measure the effect that learning one motor task can exert on the ability to learn a second motor task, subjects were tested in a second target set that began 3 to 5 minutes after the end of Task A. In this target set, or Task B, the manipulandum produced a set of forces 180° opposite to the ones applied during Task A (see Methods). Performance, as measured by the mean of the correlation coefficients, was worse in Task B than in Task A ($0.79 \pm 0.03$ vs. $0.84 \pm 0.04$; $t(7) = -5.3$, $p = 0.001$), demonstrating that the learning in Task A transfered negatively to Task B. Fig. 2-6 shows the average learning curves for the 8 subjects in Task A and Task B. It also plots the difference between the 2 curves, along with 95% confidence intervals.

NT was also apparent in the subjects' movement times and path lengths (Fig. 2-7). When switched to Task B, subjects took a longer time on their way to the targets than they did when first given Task A ($0.62 \pm 0.04$ sec vs. $0.67 \pm 0.06$; $t(7) = -2.79$, $p = 0.027$). Subjects also moved through a longer path on their way to the targets

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[1] Values given are mean ± standard deviation. For within subject comparisons, two-tailed paired t-tests were used. For between subjects comparisons, two-tailed t-tests were used.

in Task B than they did when first given Task A (10.40 ± 0.52 cm. vs. ± 0.87 cm.; $t(7) = -2.95$, $p = 0.021$).

## Discussion

The three measures of performance — correlation coefficients, movement times, and path lengths — all indicated that subjects were less able to counteract the perturbing forces in Task B than they had been in Task A. This decrement in performance was not due simply to fatigue. Pilot studies have indicated that subjects can perform in up to 3 target sets in a row and continue to improve in each one (unpublished results; also, see Experiment Two).

The correlation coefficients are, perhaps, the most sensitive of the 3 measures. This is in part because the other two measures often have a reciprocal relation in this paradigm. Since the magnitude of the perturbing forces depended on the speed of the subjects' movements, a subjects' hands were pushed harder the faster they moved. In order to reach the target within the specified time window despite the perturbations, subjects often increased the speed of their movements, increasing the perturbing forces as well. Thus, they might have reached the target within the proper time, but along a longer path. In this instance, the movement times would indicate good performance, while the path lengths would not. The correlation coefficient takes into account, among other parameters, both the length and speed of subjects' movements, providing a more sensitive measure of the effects of the perturbations.

Subjects' performances while moving to the targets in Task A when either the null or the 180° probe forces were applied provided insight into the strategies they used to compensate for the learned forces. Performance in the 180° probe forces in Task B will be examined in the discussion at the end of this chapter. Subjects could theoretically adopt either of two strategies to counteract the learned forces. They could co-contract the muscles of their arms, in essence increasing their arms' stiffness. This strategy would enable them to resist perturbations from many directions. Alternatively, subjects could learn to predict the particular forces that they expected to encounter along any trajectory. They could then produce compensatory forces that would counteract the specific forces they were learning. The aftereffects visible during the null probe targets gave a visual indication that subjects were trying to compensate for the specific learned forces. By pushing in a direction opposite to the direction the viscous forces pushed, subjects could resist the perturbations. When the forces were removed unexpectedly, the subjects overshot in the direction they had been pushing. Aftereffects have been used previously to probe the mechanisms of visuo-motor adaptation [27]. Similarly, the fact that subjects' performance in the 180° probe targets did not improve along with their performance in the learned forces indicates that subjects employed a specific predictive strategy. Had subjects increased the stiffness of their arms non-specifically, their performance would have increased no matter which forces were active during any particular movement.

# Experiment 2

## Introduction

Motor learning and memory are measured through performance. The influence of motor learning on performance can be assessed on the particular skill that was learned or on a new skill — measures of retention and transfer, respectively. The results of the previous experiment demonstrated that the acquisition of one motor skill resulted in NT when a new motor skill was learned. It is not clear whether tests of retention and transfer measure the same ability, or whether they reflect separate underlying mechanisms. One way to explore this issue is to compare the effect of time on tests of retention and transfer. If the retention interval affects the two measures differently, then it is likely that the measures reflect distinct processes.

Experiment 1 found NT in Task B 3-5 minutes after Task A was learned. Experiment 2 compared retention and NT 24 hours after subjects learned Task A.

## Method

## Subjects

Right-handed subjects (n = 20; male/female: 4/6), 18-35 years old (mean ± SD: 23.1 ± 2.8), recruited from the MIT community participated in this study. Subjects classified themselves as right-handed and reported that they did not have any neurological disorders. MIT's Committee on the Use of Humans as Experimental Subjects approved all experimental protocols.

The Apparatus and Measurements were the same as those used in Experiment 1.

## Procedure

In brief, subjects moved the handle of the manipulandum to a series of targets. Subjects were divided into 2 groups, Group 1 (n = 10; male/female: 4/6) and Group 2 (n = 10; male/female: 4/6). Both groups were tested in 3 conditions over 3 consecutive days: baseline, Task A, and Task B. Day 1, or the baseline day was identical to that in Experiment 1. On that day, the manipulandum produced no forces as subjects moved from target to target. On Day 2, subjects in both groups learned to move the manipulandum accurately as it produced one pattern of velocity dependent forces (Task A). Subjects practiced Task A for 3 target sets. On Day 3, subjects in Group 1 were tested in Task B for transfer of skill. In Task B the manipulandum produced a pattern of forces that were opposite to those in Task A. Subjects in Group 2 were retested in Task A for retention of skill. They were then tested in Task B.

**Baseline** Subjects learned the timing of the task. The torque motors did not deliver any forces to the subjects' hands. It took most subjects between 300 and 500 movements to master the task to a level at which they could reach most targets within the proper window of time. When subjects were able to move consistently to the targets at the proper speed, 12 movements in each of the 8 target directions were recorded. These 96 movements comprised the subjects' baseline trajectories, against which later performance on Day 2 would be measured.

**Task A** Subjects refamiliarized themselves with the timing of the task by moving to approximately 50 targets in the absence of the perturbing forces before testing began.

Immediately thereafter, they learned to move the manipulandum while it produced perturbing forces. The subjects' instructed goals were the same as during the baseline target session the previous day. They were told that the robot arm would push and pull their hands as they tried to move from target to target. Two torque motors delivered velocity-dependent forces to the handle of the manipulandum, perturbing the subjects' movements as they tried to guide it to the targets. For half the subects, the perturbations during the first target set used clockwise forces, and for the other half, counterclockwise forces. Subjects practiced this task, Task A, for 3 target sets. Subjects received a 3-5 minute break between target sets.

**Retention/Transfer** Both groups once again refamiliarized themselves with the timing of the task by moving to approximately 50 targets in the absence of the perturbing forces before testing began. The subjects in Group 1 were then tested in Task B. In Task B, the manipulandum produced forces 180° opposite to those the subjects had learned the previous day in Task A. The subjects in the Group 2 were retested first in Task A. That is, they moved the manipulandum to the series of targets while the manipulandum produced the same perturbations that it had produced on day 2. After a 3-5 minute break, the subjects in Group 1 were tested in Task B.

## Results

### Task A

On Day 2, performance for both groups when first exposed to the perturbing forces was similar to that of the subjects in Experiment 1, that is, the correlation coefficients for both groups increased in the first target set (Figs. 2-8 and 2-9). As in Experiment 1, the correlation coefficients for the movements to the 180° probe targets did not rise during the training set. Subjects' performances continued to rise throughout each of the 3 target sets.

### Retention/Transfer

**Group 1** On Day 3, 24 hours after they had learned Task A, the subjects in Group 1 were tested in Task B. They performed at a level almost identical to that of their initial performance in Task A the day before (Fig. 2-8). There was no significant difference between the mean performance in Task B on Day 3 and in the first target set of Task A on Day 2 as measured by the correlation coefficients (0.82 ± 0.06 vs. 0.82 ± 0.05; $t(9) = 0.35$, $p = 0.73$).

**Group 2** On Day 3, when subjects in Group 2 were retested with a single target set in the forces they had learned the day before, their mean performance as measured by the correlation coefficients was significantly higher than it had been when first exposed to the forces on Day 2 (0.87 ± 0.05 vs. 0.83 ± 0.04; $t(9) = 2.97$, $p = 0.016$). Their mean performance in Task A on Day 3 was comparable to that of the second target set on Day 2 (0.87 ± 0.05 vs. 0.88 ± 0.04; $t(9) = 0.25$, $p = 0.8$), and significantly lower than that of the third target set on Day 2 (0.87 ± 0.05 vs. 0.90 ± 0.04; $t(9) = -2.79$, $p = 0.021$).

After a 3-5 minute break, subjects in Group 2 were tested in a second target set. During this second target set, the pertubing forces were 180° opposite to the forces in the first target set. The mean performance in Task B was significantly lower than the mean performance had been during the first target set in Task A on Day 2 (0.77 ± 0.06 vs. 0.83 ± 0.04; $t(9) = -5.90$, $p = 0.0002$).

# Results from Experiments 1 and 2

The results in this section are derived from the data from Experiments 1 2. The procedures and results from Experiments 1 and 2 are summarized in Fig. 2-14.

## Negative Transfer Affects the Ability to Learn a New Task

It is not clear from the analysis so far whether NT reflected an inability to *learn* in Task B. It is possible that the overall poor performance in Task B was a function only of the fact that subjects started at a lower point on the learning curve. Subjects may have improved at a normal rate from this lower initial performance, suggesting that their ability to learn had not been affected.

In order to measure subjects' ability to learn, the improvement in performance in a target set was defined as the average of the final 40 movements minus the initial 8 movements[2] Improvement in Task B was compared to that in Task A for the 2 groups that showed NT: the group from Experiment 1 and Group 2 from Experiment 2. Improvement in the first target set in Task A was slightly but not significantly less than that in Task B (0.14 ± 0.05 vs. 0.14 ± 0.06; $t(17) = 0.75$, $p = 0.50$; Fig. 2-12).

The amount that each subject improved, however, was negatively correlated with that subject's initial performance ($r^2 = 0.38$, $F(1,24) = 14.5$, $p = 0.00086$; Fig. 2-11). This can be understood easily in terms of the "ceiling effect' imposed by the maximum value of 1 that the correlation coefficients can assume. Subjects who starged with higher initial correlation coefficients had less room for improvement. When an analysis of covariance (ANCOVA) was performed to compensate for this fact, the mean improvement in Task A was significantly higher than that in Task B (0.16 vs. 0.14; $F(1,16) = 5.71$, $p = 0.03$ Fig. 2-12).

The strategy subjects used to improve in Task A and Task B was examined. In each target set, 8 of the movements were made while the manipulandum applied forces 180° opposite to the forces subjects were learning. The subjects' performance in these 180° probe forces revealed the specificity of their improvement. To the extent that a subject was counteracting the forces by increasing the stiffness of his or her arm, he or she would have demonstrated an improved performance in either set of forces. In Task A, subjects improved only in the specific set of forces that were being applied for the majority of movements (the learned forces). Performance in the 180° probe forces remained at the initial level throughout the target set. In Task B, however, subjects reacted differently to the 180° probe forces than they had in Task A. Halfway through Task B, subjects performed at the same level regardless of which set of forces

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[2] The final 40 movements were averaged together to smooth the fluctiations many subjects exhibited around their asymptotic performance.

were being applied (Fig. 2-13). They were, therefore, adopting a non-specific strategy to compensate for the forces. The performance in the few opposite forces decreased towards the end of the target set, suggesting that the inhibitory effect NT exerted on subjects' ability to learn faded with practice.

## Relation between Level of Learning in Task A and NT

A test of linear correlation showed a non-significant relationship between the asymptotic performance in Task A and the amount of NT ($r^2 = 0.016$, $p < 0.65$; Fig. 2-15)

## Comparison of NT in the 3 Conditions

The NT, defined as the difference in mean performance in Task B and Task A, in the 3 groups of subjects from Experiments 1 and 2 amount was compared using a one-way analysis of variance (ANOVA). Using the correlation coefficients as the measure of performance, a significant difference was found between the 3 conditions ($F(2,25) = 9.73$, $p = 0.00075$). Pairwise post hoc comparisons revealed that the 2 groups that learned Task B 3-5 minutes after Task A had significantly more NT than the group that waited 24 hours between Task A and Task B ($p < 0.01$). There was no significant difference between the amounts of NT in the 2 groups that learned Task B 3-5 minutes after Task A.

# Discussion

These experiments show that NT can be a significant factor in human motor learning, affecting several aspects of learning and performance. Subjects performed at a lower level and improved at a slower rate when they tried to learn a second sensorimotor transformation shortly after they had learned a first one. They also adopted a different, less-specific strategy to compensate for the perturbations imposed on them by the motor learning task. However, the negative effect that skill in one motor task can exert on another NT was not an invariant property of the skill. Subjects retained their skill in the first task over a 24 hour period, while the NT disappered over the same time period.

The rationale behind having the subjects in Experiment 2 practice Task A for 3 target sets, instead of just one target set, as the subjects in Experiment 1 did, was as follows. The degree of learning in a first task has been shown to affect transfer in tasks of explicit learning, sometimes even turning from NT to positive transfer with increasing training in the first task [60]. It was important, therefore, in order to compare the amount of NT 24 hours after learning a first task to the amount of NT 3-5 minutes after learning a first task, that the subjects possessed an equivalent amount of skill in the 2 conditions. Pilot studies had indicated that subjects who practiced for 3 target sets would perform after 24 hours at a level equivalent to that of subjects 3-5 minutes after they practiced for 1 target set. In Experiment 2, the level of skill in Task A that the subjects in Group 2 retained when tested on Day 3 did indeed turn out to be equivalent to that they possessed during the 2nd target set on Day 2. It can be assumed, therefore, in Experiment 2 that, when the subjects in Group 1 were tested on Day 3 in Task B, they retained an amount of skill in Task A equivalent to that possessed by the subjects in Experiment 1. The fact that the Group 1 subjects in Experiment 2 showed no NT, while the subjects in Experiment 1 did, can not be attributed to any differences in the amount of skill in Task A.

It is interesting to note in this context that the amount of NT did not seem to depend on the level of proficiency subjects attained in Task A. In the one previous study that examined this issue in a motor learning task [34], the degree of training in a first task has not affected the amount or sign of transfer. This is in contrast to the results in explicit learning tasks [60].

Osgood's surface of retroaction [49] would predict that the experimental design used in this study should result in NT. The visual stimuli — the targets — were identical in Task A and Task B. The response required of the subjects, however, were dissimilar in the two tasks. The pattern of muscular activations needed to move the subjects' right arms to the targets in the clockwise and counterclockwise forces were quite different. Similar stimuli and dissimilar responses, according to Osgood, should lead to NT. Although this S-R explanation can explain and even predict the results of Experiment, the effect of time shown in Experiment 2 would not be predicted on the basis of an associationist interpretation. Since subjects retained their skill in Task A, they could be said to have retained their S-R associations. There is no way that this theory can account for the fact that the S-R associations that are present 3-5 minutes after learning Task A cause NT, while the S-R associations that are present 24 hours after learning Task A do not.

Motor memory is not a unitary phenomenon. The results presented in these experiments suggest two possible models (Fig. 2-16). In the first, two effects are created as a result of motor learning. The first is skill in the practiced task. This is what is commonly referred to as motor memory. The second effect is NT. Motor memory is retained for at least 24 hours. NT decreases with time, disappearing within 24 hours. In this model, both effects are created when learning occurs. One endures, whereas the other does not.

The second possible model is a consolidation model. The motor memory is transformed with time from a state in which it causes NT to one in which it does not cause NT. In this model, the way the motor learning is stored changes with the passage of time. The nature of this change is not revealed by these experiments, but possibilities include a change in anatomical locus or a change in the biochemical substrate in which the learning is embedded.

The results presented in this chapter are not sufficient to distinguish between these two models. The next chapter presents data that suggest the consolidation model is the more likely.

# Figures

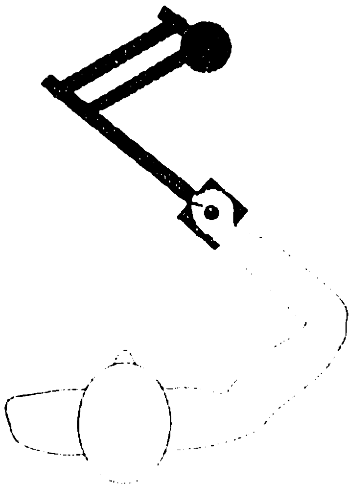


Figure 2-1: **The experimental setup.** The two-link planar manipulandum was equipped with two motors that could deliver torques independently to either of the the two joints of the manipulandum.

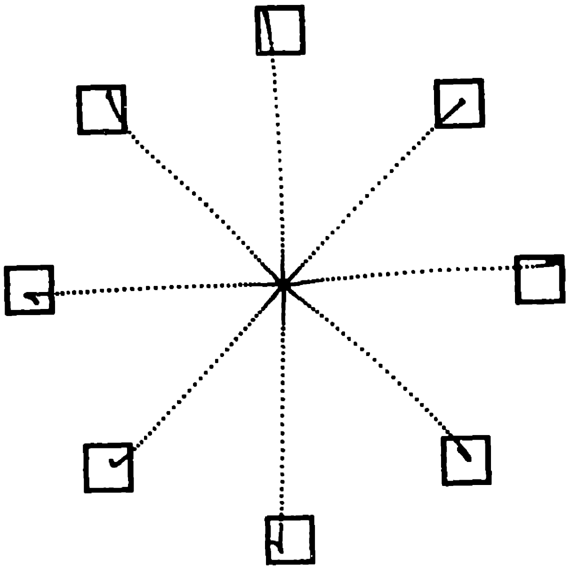


Figure 2-2: **Typical baseline trajectories for one subject.** For ease in displaying the trajectories, a movement towards the center target from one of the outward targets was plotted as if it were a movement out from the center. For example, a movement to the center from the upward target was displayed as if it were a movement from the center downward.

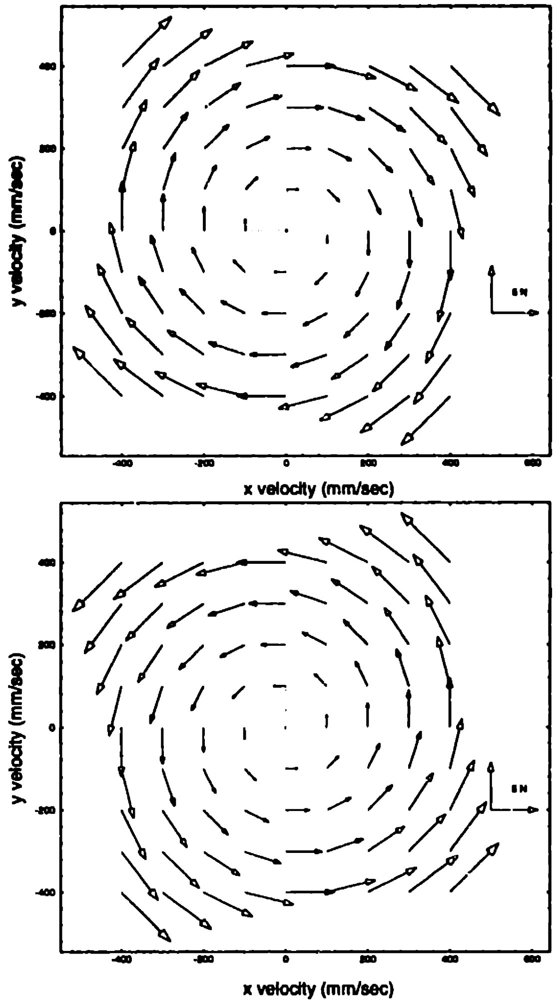


Figure 2-3: **Clockwise (top) and counter-clockwise (bottom) sets of velocity-dependent forces used in this study.** The forces are plotted in velocity space. The direction and length of an arrow indicate the direction and magnitude of the forces at that location in velocity space.

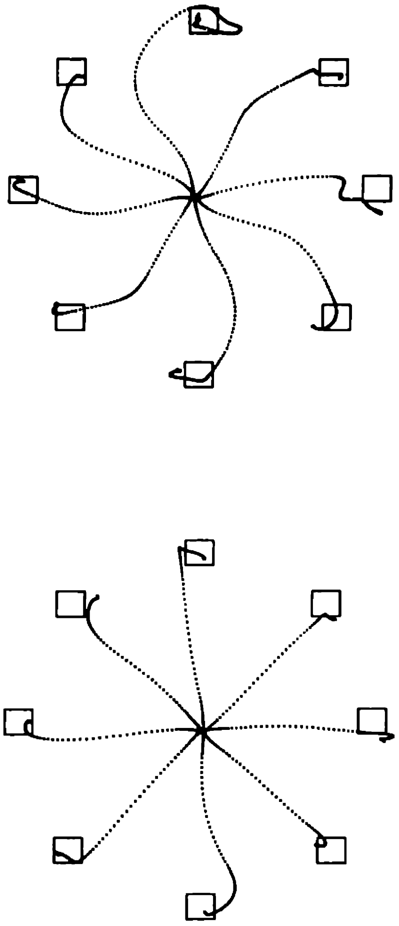


Figure 2-4: **Trajectories for a typical subject.** On the top, the subject's trajectories to each of the 8 targets when the perturbing forces were first turned on. For this subject, the forces were in the counter-clockwise direction. On the bottom, the same subject's trajectories, still in the presence of the same forces, but after approximately 5 minutes of practice.

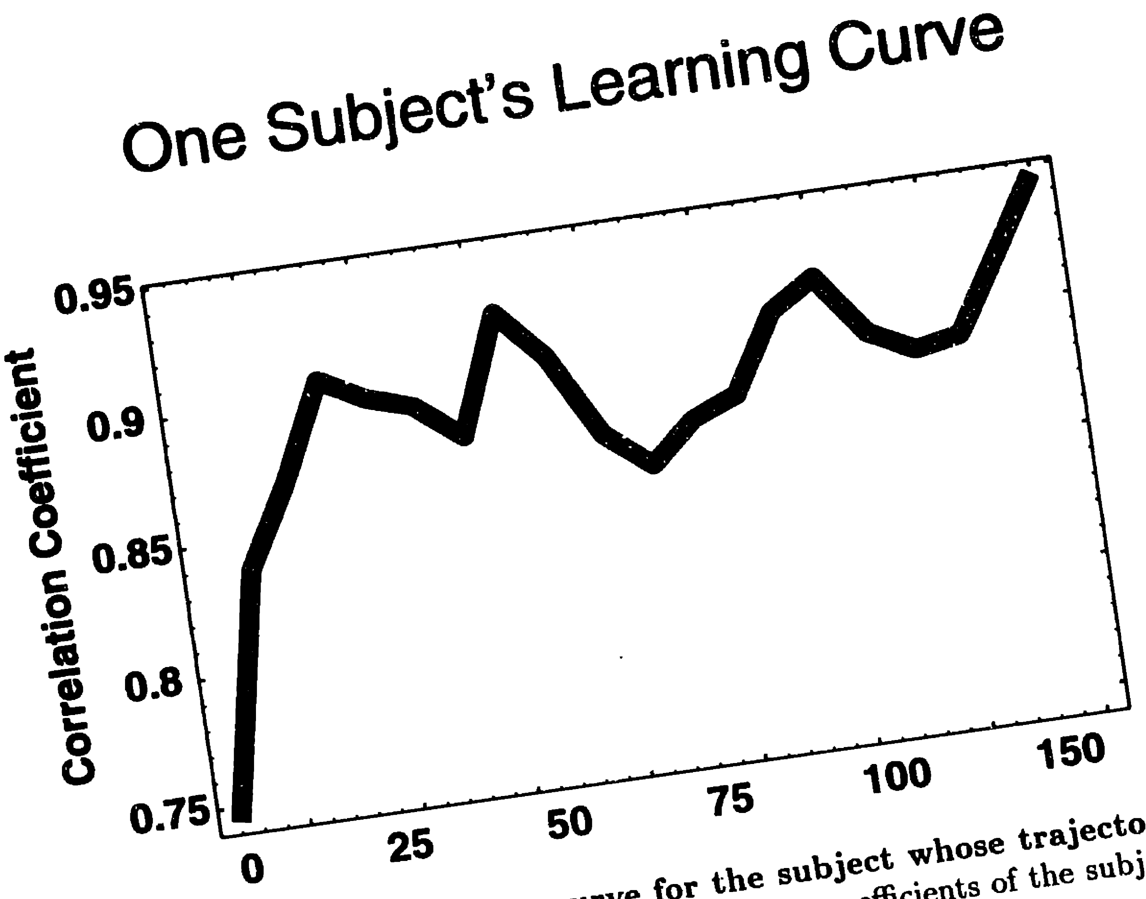
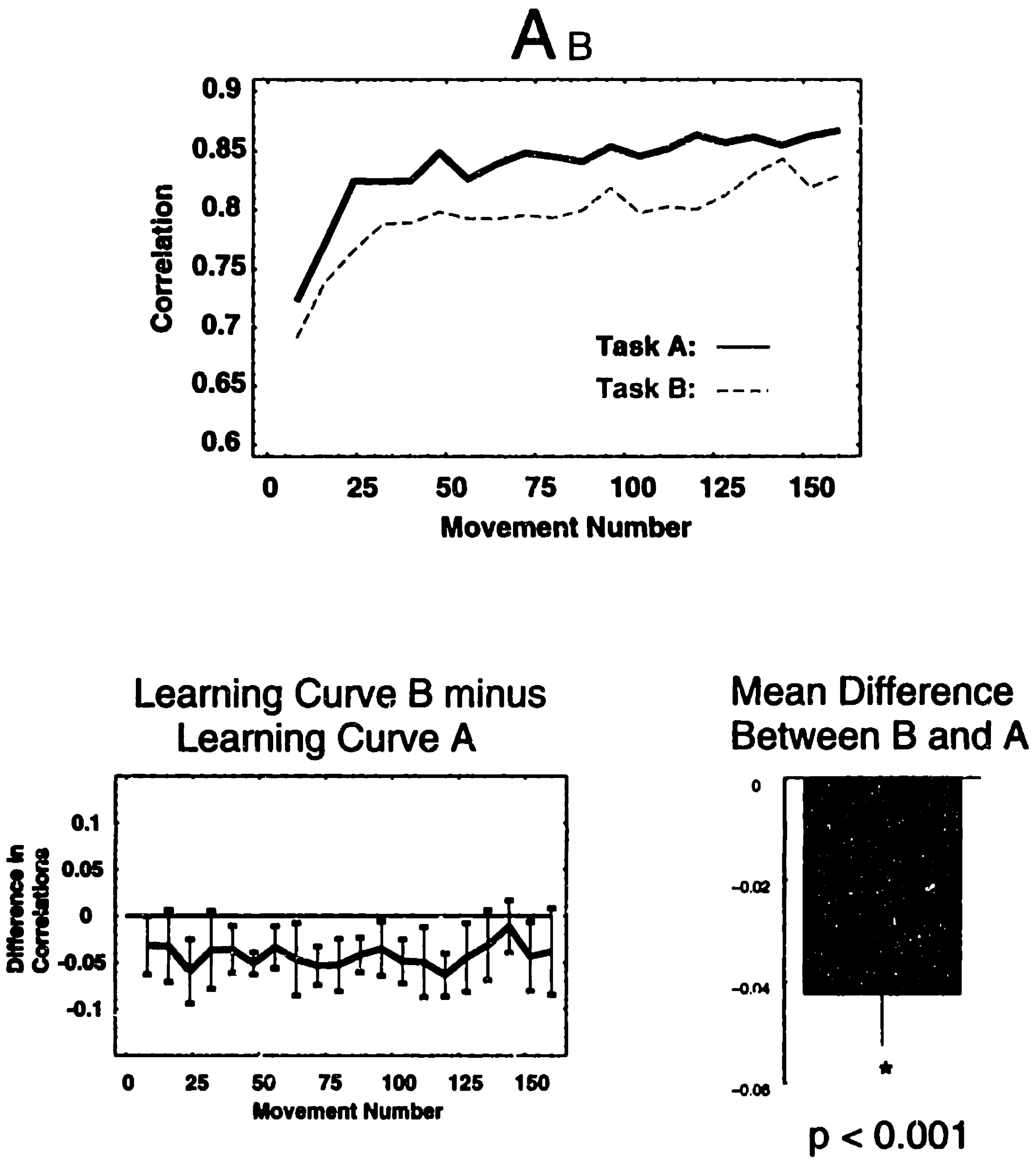


Figure 2-5: **A plot of the learning curve for the subject whose trajectories were shown in the previous figure.** The correlation coefficients of the subject's trajectories are plotted against the number of the subject's movements.



Learning Curve B minus Learning Curve A

Mean Difference Between B and A

Figure 2-6: **Data demonstrating NT.** The upper figure shows the learning curves for these subjects as they practiced Task A (dark, solid line) followed 3 to 5 minutes later by Task B (light, dashed line). Performance in Task B was consistently lower than performance in Task A. The lower left graph shows this difference directly, along with 95% conficence intervals. The lower right bar shows the mean difference between the performance in Task A and Task B. This difference was significantly different from zero. In this and the following figures, the experimental procedure subjects followed is depicted schematically at the top of the figure. The letters A and B stand for Tasks A and B, respectively. The size of each letter indicates the level of performance acheived in that target set.

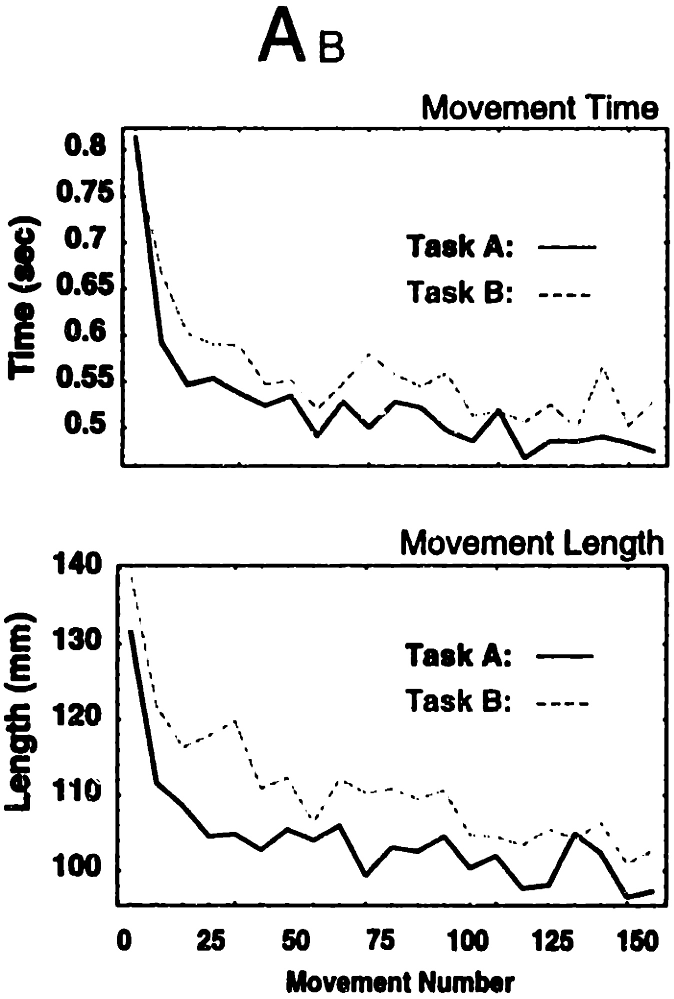


Figure 2-7: **Graphs of movement times (top) and path length (bottom).** The mean movement time and path length in Task B were significantly longer than in Task A ($p < 0.02$ and $p < 0.01$, respectively)

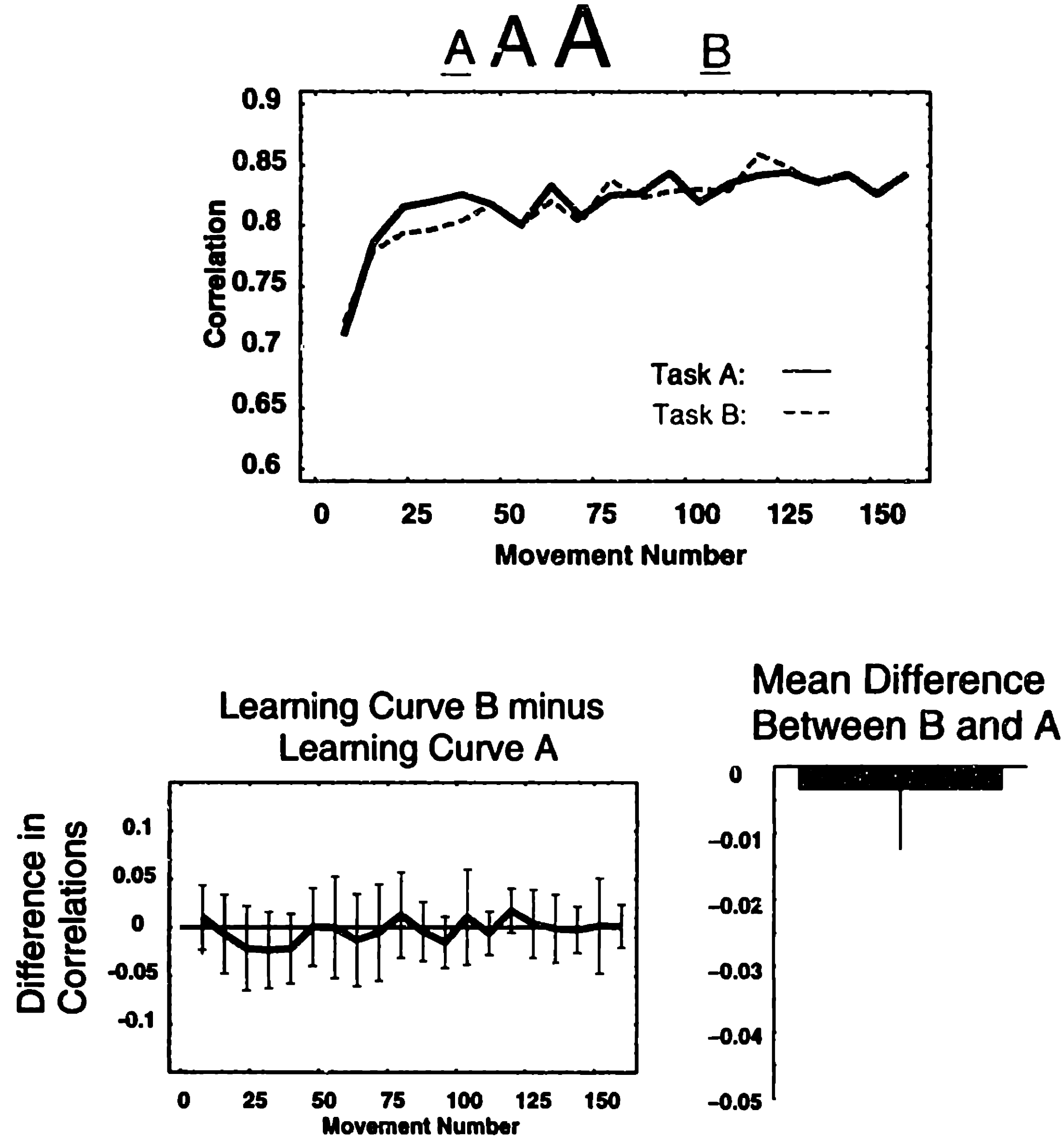


Figure 2-8: **Data demonstrating the disappearance of NT in Group 1.** The upper figure shows the learning curves for these subjects as they practiced Task A (dark, solid line) followed 24 hours later by Task B (light, dashed line). Performance in Task B was nearly identical to performance in Task A. The lower left graph shows this difference directly, along with 95% conficence intervals. The lower right bar shows the mean difference between the performance in Task A and Task B. This difference was not significantly difference from zero ($p > 0.5$. In this and the following figures, the target sets that are compared in the graphs are indicated by underlines in the schematic summary of the experimental protocol at the top of page. The space between the third "A" and the "B" indicates a break of 24 hours.)

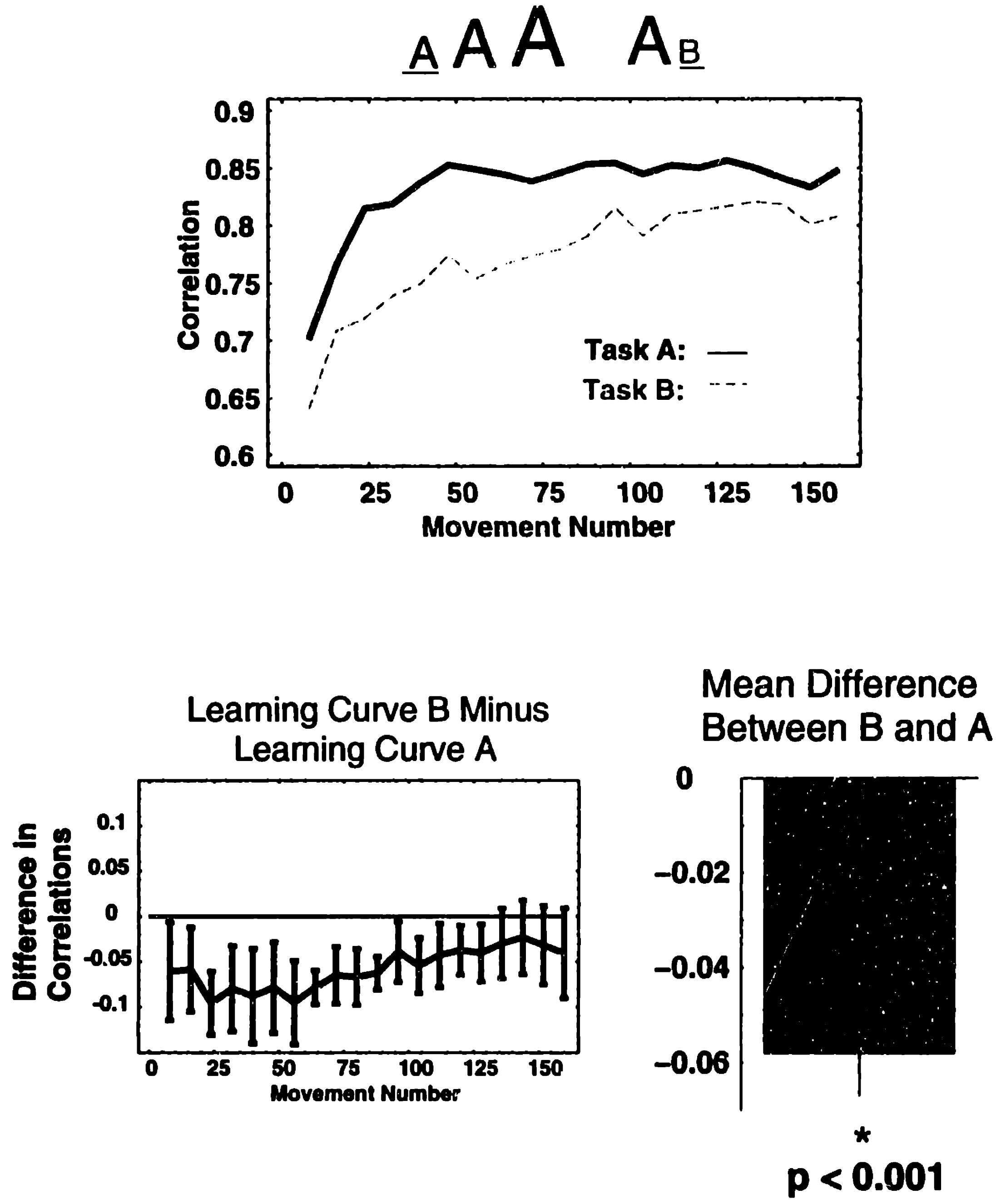


Figure 2-9: **Data demonstrating the reappearance of NT in Group 2.** The upper figure shows the learning curves for these subjects as they practiced Task A on Day One (dark, solid line). They then practiced Task A again 24 hours later (not shown), followed 3 to 5 minutes later by Task B (light, dashed line). Performance in Task B was significantly worse than the original performance in Task A. The lower left graph shows this difference directly, along with 95% conficence intervals. The lower right bar shows the mean difference between the performance in Task A and Task B. This difference was significantly difference from zero ($p < 0.001$).

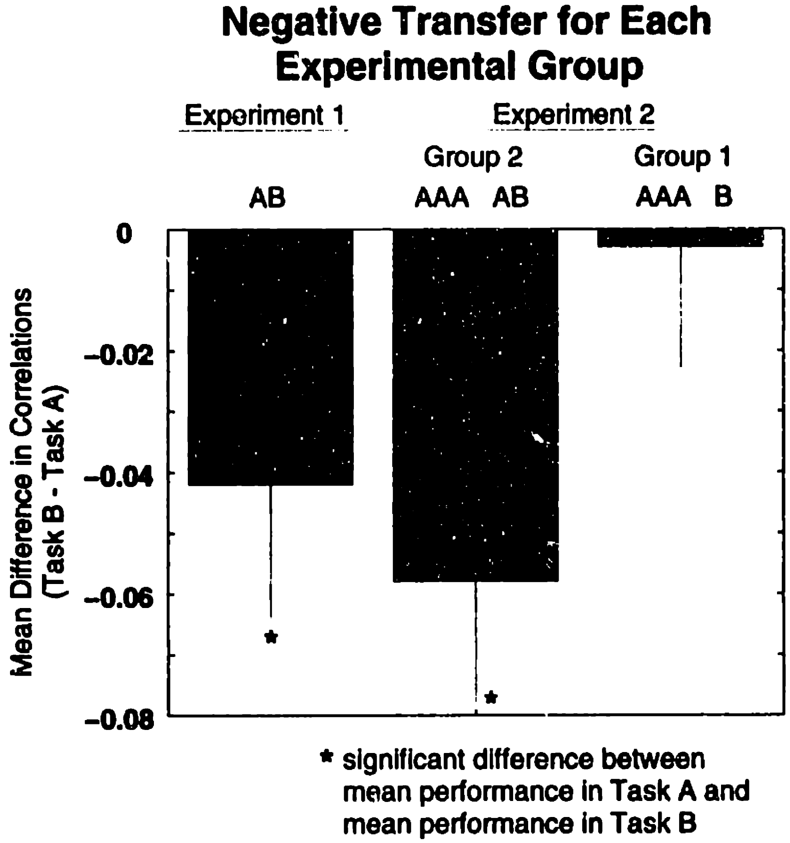


Figure 2-10: **NT for the 3 experimental groups.** The experimental protocol under which each group was tested was summarized under the group labels. Both Group 1 and Group 3 showed NT: the mean performance of these 2 groups in Task B was significantly less than in Task A ($p < 0.001$). Group 2 did not demonstrate any NT. There was also a significant difference between the groups in the mean difference in correlations in Task A to Task B ($F(2,25) = 9.72$, $p < 0.0001$).

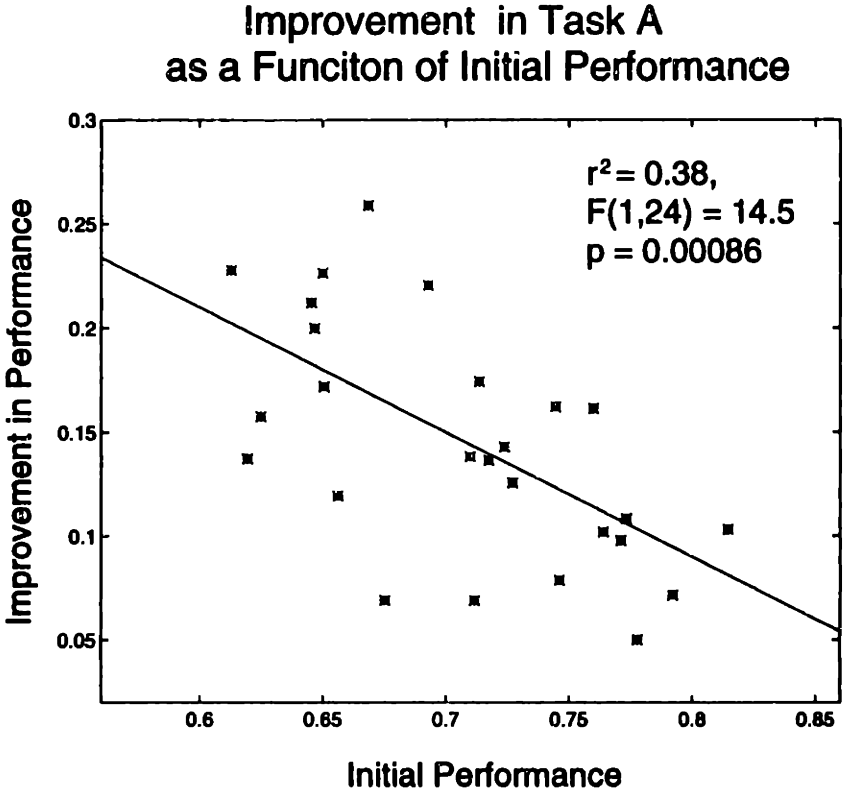


Figure 2-11: **Relation between improvement in Task A and the initial performance in Task A.** The performance in Task A for all subjects in Experiments 1 and 2 were included in this figure.

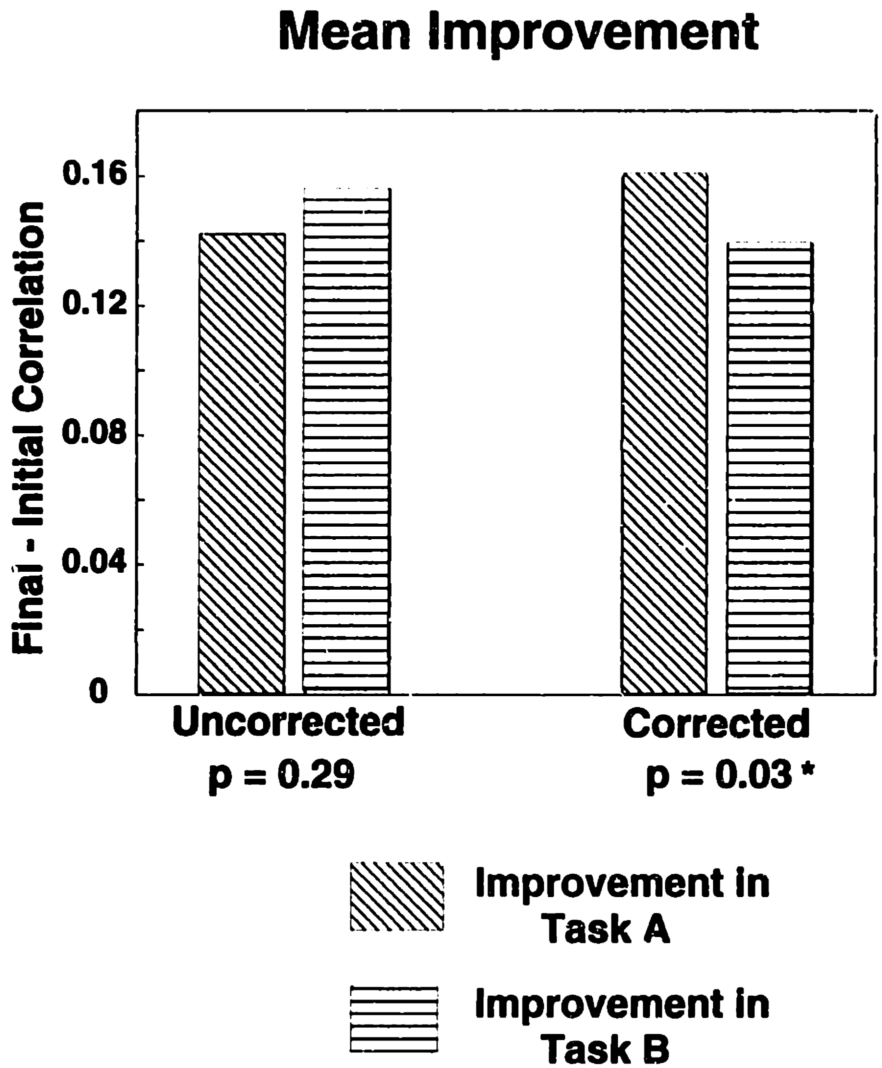


Figure 2-12: **Final - initial performance in Task A and Task B for the two groups that displayed NT.** There was no significant difference between the two values before correction for level of initial performance ($p < 0.5$). However, when improvement was covaried for initial performance, improvement in Task B was significantly less than in Task A.

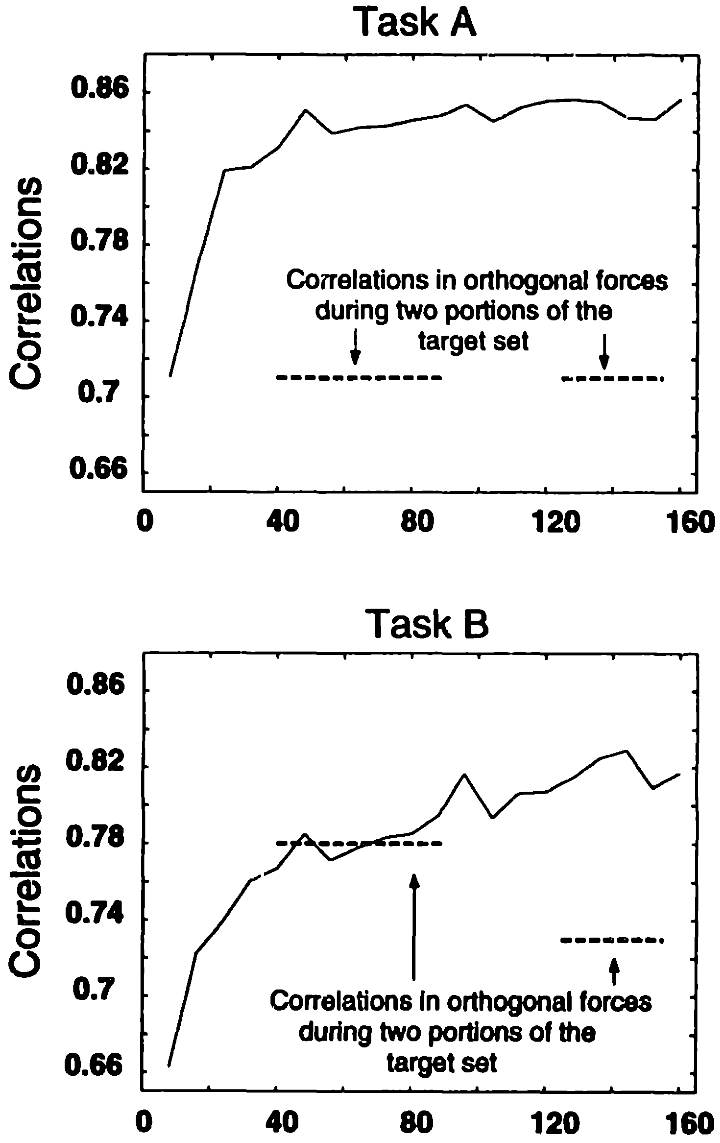


Figure 2-13: **Comparison of the specificity of learning in Task A and Task B.** Performance in the 180° probe targets indicates that subjects in Task B initally employed a non-specific strategy to counteract the forces.

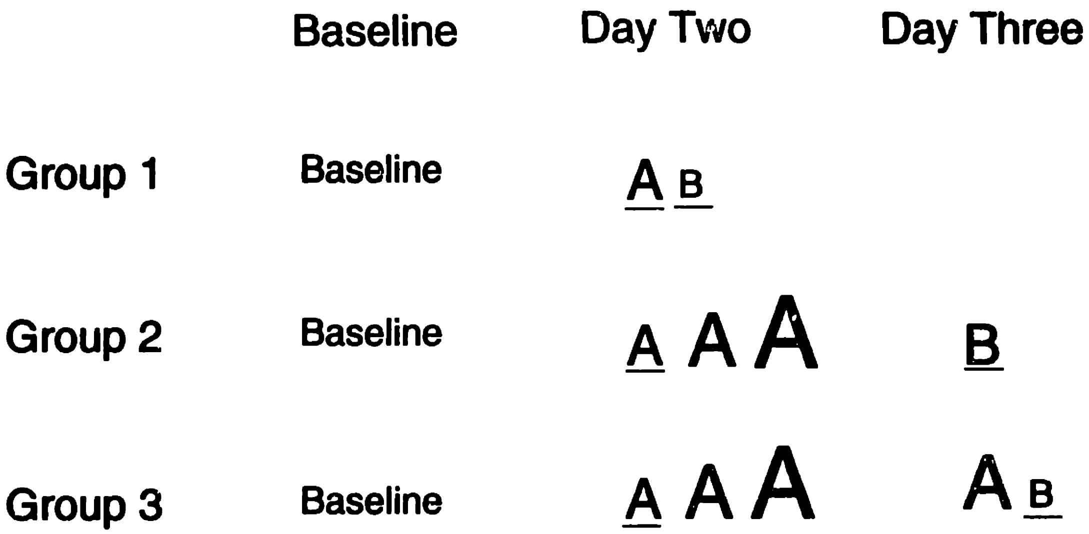


Figure 2-14: **Treatment protocols for the 4 subject groups.** Each letter "A" indicates that subjects learned Task A for one target set (92 targets, approximately 5 minutes). The letter "B" indicates that subjects learned Task B for one target set. See the text for an explanation of the different tasks. The size of the letters represents the level of skill subjects attain in each target set. The larger letters indicate superior performance. The underlines call attention to the target sets that were compared when measuring NT.

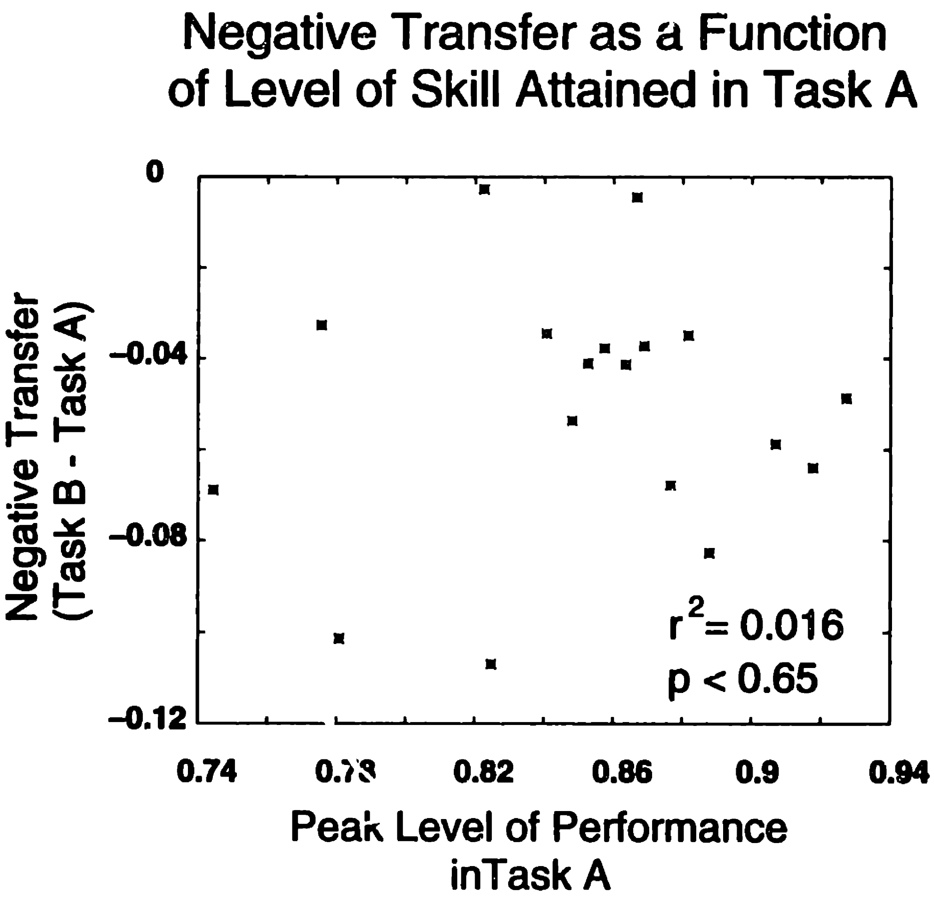


Figure 2-15: **Plot of the magnitude of NT in each subject as a function of the level of performance that subject reached in Task A.**

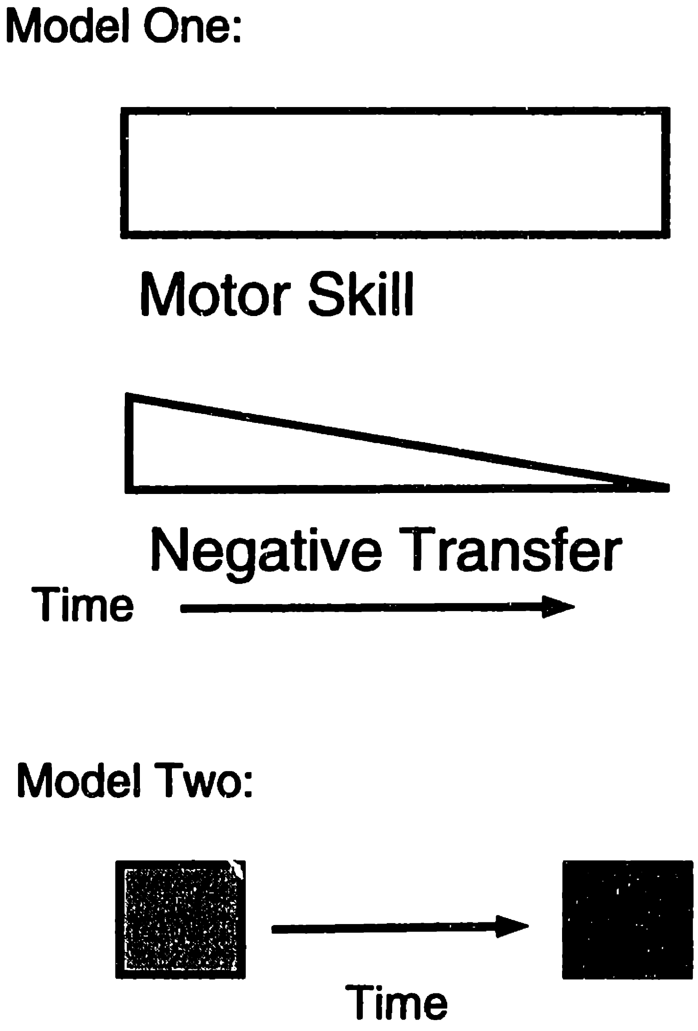


Figure 2-16: A schematic depiction of two models that account for the experimental results presented in this chapter.

# Chapter 3

# Consolidation in Human Motor Learning

## Abstract

**Learning can set in motion neural processes that continue to evolve for a period of time after practice on a task has ended [9, 33, 39, 67, 71]. This phenomenon is known as consolidation [39, 67, 71]. The experiments in Chapter 2 explored the time course of the consolidation of motor learning. Right-handed subjects (n = 60; male/female: 2/1) 18-35 years old (mean ± SD: 23.4 ± 4.4), learned to control the manipulandum while it perturbed their movements with one pattern of forces as described in Chapter 1. They then learned to guide the manipulandum while it produced a second pattern of forces. This second pattern was learned either immediately after the first pattern or after a break of either 4 or 8 hours. When subjects learned the two different patterns of forces, one immediately after the other, they experienced a mutual interference between the tasks: performance in the second task was reduced in all subjects, and 24-hour retention of the first task was virtually eliminated. By contrast, the subjects who waited either 4 or 8 hours between learning the first and second patterns showed significantly less of both types of interference. The**

motor memory had consolidated within 4 to 8 hours. The disruption of consolidation through specific behavioral interventions has been shown to occur in explicit memory, which depends on different neural structures than motor memory [44, 15]. By extending this phenomenon to motor memory, these results suggest that distinct neural systems share similar characteristics when encoding and storing new information.

The results presented here provide the first demonstration that the consolidation of human motor memory can be disrupted through behavioral means in a time-dependent manner. When subjects learned two different motor tasks, one immediately after the other, they experienced a mutual interference between the tasks: performance in the second task was reduced in all subjects, and 24-hour retention of the first task was virtually eliminated. By contrast, subjects who waited either 4 or 8 hours between learning the first and second tasks showed significantly less interference. The disruption of consolidation through specific behavioral interventions has been shown to occur in explicit memory, which depends on different neural structures than motor memory [44, 15]. By extending the phenomenon of consolidation to motor memory, these results suggest that distinct neural systems share similar characteristics when encoding and storing new information.

## Introduction

Research over the past century has converged to indicate that certain types of memory undergo a time-dependent process of consolidation [61, 38]. These memories exist initially in a vulnerable state, where they can be disrupted by a variety of interventions. The interventions can be specific to the task learned. For example, learning a second similar task soon after the learning the first task can disrupt the consolidation process, whereas learning a second, non-similar task will not [49, 51]. Retrograde interference (RI) is said to have occured when learning a second task interferes with the retention of a previously learned task. The interventions can also be more general, such as electroconvulsive shocks [40] and inhibition of protein synthesis.

If disruption of consolidation does not occur, the memory can be transformed with the passage of time to a long-term, less fragile state. One common feature of the many different protocols is that the effectiveness with which the interventions disrupt memories depends, in part, on the amount of time that passes between their application and the original learning. This phenomenon has been called the temporal gradient of retrograde amnesia [61]. This temporal gradient forms the basis of the consolidation theory. The consolidation theory postulates that the neural form in which the memory is stored is altered during the hours and days after the memory is acquired. This alteration, or consolidation, leaves the memory less vulnerable to disrupting interventions.

Consolidation has been reported in a number of animal species and with several types of learning. Animals studied have included mice, rats, goldfish, monkeys, and fruit flies; and learning paradigms have included maze learning, passive and active avoidance, operant responses, and delayed non-matching to sample tasks [17, 3, 67, 74, 4]. However, motor memories have been thought to be different. Motor memories have proven difficult to disrupt [28], leading to the conclusion that they change very little from the moment they are formed. The studies that have claimed to have shown motor memories to be vulnerable to disruption have not shown that the vulnerability changes with the passage of time; that is, these studies have not shown that the motor memories consolidate [34, 36, 1], even though they employed protocols that would have demonstrated consolidation of explicit memories. The procedures used in the motor studies of RI, however, have been seriously flawed. The nature of these flaws will be explained in the discussion at the end of Experiment 1.

In the present study, we investigated the question of whether consolidation occured in a motor task that required implicit adaptation to perturbing forces. Experiments 1a and 1b were conducted with the goal of determining whether RI could occur in a motor learning task. Experiment 1a examined whether learning a second, intervening task could interfere with subjects' retention of a newly learned motor skill. Experiment 1b investigated whether the nature of the intervening task was a factor in its influence on consolidation. Experiment 2 investigated the effect on RI of when the intervening task was learned in relation to the first task. There will be a discussion of the results at the end of each experiment. There will be an analysis comparing data from each experiment after they have all been presented.

The results indicated that motor memories do change in a time-dependent manner. When first formed, motor memories can be disrupted by the interpolation of a second motor learning task. This is no longer the case if 4 to 8 hours elapse before the second task is learned.

# Experiment 1a

## Method

### Subjects

Naive volunteers (n = 24) were drawn from the MIT community. Subjects classified themselves as right-handed and reported that they did not have any neurological disorders. Subjects were between the ages of 18 and 35, with a mean age of 23.2 years and a standard deviation of ± 4.1 years.

### Apparatus

Subjects sat on a chair with an adjustable height. An adjustable sling suspended from the ceiling supported subjects' right arms in the vhorizontal plane. Subjects held the handle on one end of a two-link, planar manipulandum with their right hands (Fig. 2-1) [16]. Two torque motors (PMI Corp.) controled the two joints of the manipulandum. The torque motors were used to deliver forces through the manipulandum to the subjects' hands. The forces were calculated as a function of the velocity of the hand in cartesian coordinates: $f = \mathbf{B}\dot{x}$. The matrix $\mathbf{B}$ was either $\begin{bmatrix} 0 & 13 \\ -13 & 0 \end{bmatrix} N \cdot sec/m$ or $\begin{bmatrix} 0 & -13 \\ 13 & 0 \end{bmatrix} N \cdot sec/m$. These matrices defined clockwise and counter-clockwise curl fields in velocity space, respectively (Fig. 2-3). Optical encoders and tachometers recorded the position and velocity, respectively, of the manipulandum's joints at 100 Hz. These data were transformed through a simple algorithm implemented in the software to provide the position and velocity of the handle at the end of the manipulandum.

A video display monitor, mounted above the base of the manipulandum, faced the subjects. A Gateway 2000 P5-66 computer controlled the manipulandum and the video display monitor.

### Procedure

In brief, subjects moved the handle of the manipulandum to a series of targets. Subjects were divided into 2 groups, Group 1 (n = 12; male/female: 8/4) and Group 2 (n = 12; male/female: 8/4). After a period of initial, non-recorded practice, subjects were tested in 3 conditions over 3 days. On the first day, subjects in both groups practiced the timing of the task. Baseline recordings were then made. The manipulandum produced no forces. On the second day, both groups learned to move the manipulandum accurately as it produced one pattern of velocity dependent forces (Task A). Group 2 then went on to learn Task B, in which the manipulandum produced a pattern of forces that were opposite to those in Task A. On the third day, both groups were retested in Task A.

**Initial Practice** Subjects moved the handle of the manipulandum to guide a cursor to a series of targets that appeared one at a time on the computer monitor. The torque motors did not deliver any forces to the subjects' hands. The cursor started at the center of the monitor and remained visible on the screen throughout the session. Subjects moved the handle 10 cm to targets that appeared in one of eight directions: four directions starting from the center of the monitor (0°, 45°, 90°, 135°) and the four corresponding directions back to the center from each of those targets (180°, 225°, 270°, 315°; Fig. 2-2). A target set consisted of 192 targets and lasted approximately 5 minutes, the exact duration depending on each subject's movement times. Targets out from the center of the monitor were always followed by a target at the center. After the subject stopped the cursor at a target, that target disappeared and the next one appeared. The targets appeared in a pseudo-random order, constrained only in that subjects made a movement in each of the 8 directions 24 times during the target set.

Subjects were instructed to keep three goals in mind as they moved the handle from target to target. First, they were told that they should wait until a target appeared before starting a movement. Second, they were asked to move at a steady, experimenter-defined pace. To provide subjects with feedback on their movement times, the computer generated a short, distinctive buzzing sound if subjects reached the target within the goal of 500 ± 50 msec. Each movement was timed with a velocity threshold that indicated when subjects started that movement, not from the appearance of the target. A target turned blue if subjects reached it after 550 msec and red if they reached it before 450 msec. It took most subjects between 300 and 500 movements to master the task to a level at which they could reach most targets within the proper window of time. Third, subjects were asked to move in a straight line from target to target.

**Baseline** When subjects were able to move consistently to the targets at the proper speed, 12 movements in each of the 8 target directions were recorded. These 96 movements comprised the subjects' baseline trajectories, against which later performance on day 2 would be measured.

**Task A** On the second day, subjects were allowed to refamiliarize themselves with the timing of the task by moving to approximately 50 targets in the absence of the perturbing forces before testing began. Immediately after this, they were presented with the task of learning to move the manipulandum while it produced perturbing forces. The subjects' instructed goals were the same as during the baseline target session the previous day. The subjects were told that the robot arm would push and pull their hands as they tried to move from target to target. Two torque motors delivered velocity-dependent forces to the handle of the manipulandum, perturbing the subjects' movements as they tried to guide it to the targets. For half the subects, the perturbations during the first target set used clockwise forces, and for the other half, counterclockwise forces. Subjects practiced this task for one target set. This target set and pattern of forces will be refered to as Task A, regardless of the direction of the forces. Subjects in Group 1 were dismissed for the day, while those in Group 2 went on to learn Task B.

**Task B** With no pause after Task A, subjects in Group 2 were given a second target set. During this second target set, the pertubing forces were 180° opposite to the forces in the first target set. If a subject was perturbed with clockwise forces during the first target set, s/he was perturbed with counterclockwise forces during the second target set, and *vice versa.* This target set will be referred to as Task B, regardless of the direction of the forces during each set.

**Retention** On the third day, both groups once again refamiliarized themselves with the timing of the task by moving to approximately 50 targets in the absence of the perturbing forces before testing began. They were then retested in Task A.

**Probe Targets** Eight of the targets out from the center intermixed throughout each set were presented without velocity-dependent forces and eight were presented with forces that were 180° opposite to the forces given in the other 176 movements. For example, if a subject's movements were perturbed by the clockwise forces for 176 movements in one target set, the forces would be turned off for 8 movements and counterclockwise forces would be applied for 8 movements spread throughout the target set. These targets will be referred to as null probe and 180° probe targets, respectively. These 16 targets were used to probe subjects' strategies in compensating for the forces (see Discussion section, and [57]). The forces that were present during the 176 targets that were neither null probe nor 180° probe targets will be called the learned forces.

## Measurements

**Correlation Coefficient** Subjects' learning was assessed using a measure of correlation that assigned a numerical value to the similarity between a subject's movements on day 2 in the presence of the perturbing forces and his or her baseline movements on day 1 (before the forces were turned on). This correlation measure revealed the extent to which a subject had adapted to the forces. The application of this measure has been validated in previous work, where it has been shown that, as a subject practices moving the handle of the manipulandum while it produces perturbing forces, his or her trajectories converge to those of the baseline [57]. The correlation coefficient captures this convergence.

The correlation coefficient, $\rho$, between two trajectories, $a$ and $b$, is the ratio of the covariance between $a$ and $b$ and the product of their standard deviations: $\rho(a,b) = \frac{\mathrm{Cov}(a,b)}{\sigma(a)\sigma(b)}$. $\rho$ can take a value from $-1$ to 1, with 1 indicating that two trajectories are identical, and -1 indicating that they move in 180° opposite directions.

## Criteria for Exclusion from Analysis

In order for the measure of correlation to accurately reflect a subject's learning, it is important that the subject try to replicate his or her movements from one session to the next. A small percentage of subjects disregarded the instructions to move at a steady pace from target to target. To identify these subjects objectively, the average peak velocity of a subject's trajectories in the baseline condition and in the various learning tasks was calculated. The ratio of the average peak velocity in the learning tasks to that of the baseline condition provides an indication of the amount by which a subject alters the speed of his or her trajectories from one condition to the next. Subjects whose ratios departed from the mean of all subjects' ratios by more than two standard deviations were excluded from further analysis. By these criteria, we excluded 4 of 60 subjects from our analysis in the three experiments. One subject was excluded from Group 2 in Experiment 1a; 2 were excluded from Group 1, and 1 from Group 2 in Experiment 2.

# Results

## Task A

**Improvement in Task A** The performance in Task A of subjects from both groups was very similar to that reported in the previous chapter. When first exposed to the forces, subjects' movements deviated from the straight-line trajectories of the baseline (compare Fig. 3-2a and c). After 5 minutes of practice, most subjects were able once again to move in a fairly straight line to the targets (Fig. 3-2d). The improvement in performance over the target set was significant for both groups (**Group 1:** initial correlation vs. final correlation: 0.75 ± 0.07 vs. 0.89 ± 0.03; $t(11) = 9.9$, $p < 0.000005$; **Group 2:** 0.72 ± 0.05 vs. 0.87 ± 0.05; $t(10) = 10.2$, $p < 0.000005$)[1]. The amount that subjects in Group 1 improved was not significantly different from the amount that subjects in Group 2 improved (0.15 *pm* 0.05 vs. 0.14 ± 0.05; $t(21) = 0.44$, $p = 0.67$). There was also no difference between the groups in their mean performances in Task A (Group 1 vs. Group 2: 0.86 ± 0.04 vs. 0.85 ± 0.04; $t(21) = 0.94$, $p = 0.36$).

**Null and 180° Targets** Subjects' performance in the null and 180° targets were also similar to what was reported in the previous chapter. During the null probe tarets, subjects displayed aftereffects. In contrast to the rise in the correlation coefficients in the learned forces, performance in the 180° targets did not improve throughout the target set.

## Task B

**Improvement in Task B** The subjects in Group 2 were tested in a second target set immediately after Task A. In this target set (Task B), the manipulandum produced a force field opposite tc the one applied during Task A. Subjects' performances were worse throughout almost all of Task B than their performances had been in Task A

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[1] All within group comparisons were made with paired t-tests

(Fig. 3-4). This negative transfer (NT) from Task A to Task B was seen also in the experiments reported in the previous chapter. The mean performance of the subjects in Task B was significantly less than that in Task A (0.79 ± 0.0.05 vs. 0.85 ± 0.04; $t(10) = 6.0$, $p = 0.00014$).

### Retention

On the third day, both Group 1 and Group 2 were tested for retention of Task A (Fig. 3-3). The mean performance of Group 1 when retested in Task A was significantly higher than it had been on the previous day (0.91 ± 0.03 vs. 0.86 ± 0.04; $t(11) = 8.4$, $p = 0.000004$). By contrast, Group 2 did not perform, on average, any better in Task A than they had on the previous day (0.86 ± 0.05 vs 0.85 ± 0.04; $t(10) = 0.63$, $p = 0.54$; Fig. 3-3). Only the very first movements in the retention test differed significantly from the corresponding movments during initial learning (0.81 ± 0.04 vs 0.72 ± 0.06; $t(10) = 6.5$, $p = 0.00011$). The improvement in mean performance from initial learning to retesting was significantly higher in Group 1 than in Group 2 (0.043 ± 0.02 vs. 0.005 ± 0.03; $t(21) = 3.9$, $p = 0.0009$).

## Discussion

The results of Experiment 1a provide clear evidence for RI in a motor learning task. While there have been numerous studies of RI in explicit learning tasks in humans [13, 21, 26, 30, 42, 43, 68, 69], RI in motor learning has been reported far less frequently and mostly by one group of researchers [34, 36, 35]. The experimental procedure utilized by this group was flawed to a great enough extent that one should accept their claims that they observed RI with a good deal of caution. Their procedure could not distinguish between NT and RI. Their subjects learned to move a joystick with their right hands and a pedal with their feet. These movements controlled moved determined which of a number of lights on a display panel were illuminated. The subjects' goal was to match the pattern of lights they controlled to a succession of experimenter controlled lights. Subjects practiced this task for 5 days in a row. Then subjects practiced the same task for a variable number of days, but with the mapping between their movements and the illuminated lights altered. There were 2 findings relevant for the experiments presented in this paper. First, subjects produced far more errors in the second task than they had in the first task (NT). Second, when subjects returned to the first task, they produced more errors than a control group that never learned the second task. It is this second finding that the authors reported as evidence of RI. However, the first finding makes that interpretation problematic. It is quite possible that the difficulty subjects displayed when they returned to the first task after having learned the second task was due to NT of the second task on the first. This difficulty arises because the subjects were retested in the first task under condition that had been shown to cause NT. Therefore, any decrement in performance upon being retested in the first task could be attributed to NT. In fact, some authors have gone so far as to classify RI as a form of NT [56].

It is possible, however, to design a study that can differentiate NT from RI. The experiments presented here were conducted with this in mind. Results from Chapter 1 indicate that NT in the tasks studied here does not persist over a 24 hour retention interval. Therefore, any decrement in performance on Task B during retesting in Task A on the final day could not have been caused by NT. That is, the effect of Task B on Task A must have been in the retrograde, and not the anterograde, direction.

# Experiment 1b

## Introduction

The goal of Experiment 1b was to determine whether RI could be induced merely by engaging the motor apparatus in a series of well-learned, repetitive movements immediately following the original learning of Task A. To that end, 12 subjects were tested in a protocol very similar to that in Experiment 1a. The interfering Task B in Experiment 1b required subjects to move the manipulundum to a series of targets for one target set; but in this instance, in contrast to Experiment 1a, the manipulandum produced no perturbing forces.

## Method

### Subjects

Naive volunteers (n = 12; male/female: 8/4) were drawn from the MIT community. Subjects classified themselves as right-handed and reported that they did not have any neurological disorders. Subjects were between the ages of 18 and 35, with a mean age of 22.9 years and a standard deviation of ± 4.7 years.

The apparatus and measurements were identical to those used in Experiment 1a. The procedure was nearly identical to that of Group 2 in Experiment 1a and so will be described only briefly here.

### Procedure

Subjects were tested over 3 days. On the first day, they engaged in a period of initial practice, after which they performed in the baseline task. On the second day, subjects learned to move the manipulandum while it produced perturbing forces (Task A). Immediately after learning Task A, the subjects engaged in an interfering Task B. Task B consisted of moving the manipulandum to one set of targets with no perturbing forces. Following Task B, the subjects were dismissed for the day. On the third day, subjects were retested for one target set in Task A.

## Results

## Task A

Subjects' correlation coefficients improved significantly during the training set from their initial to final values (0.72 ± 0.05 vs. 0.86 ± 0.06; $t(11) = -7.6$, $p = 0.00001$).

### Task B

When the forces were turned off for Task B, subjects continued to exhibit aftereffects for up to 10 movements 3-7. Since manipulandum did not produce any perturbing forces, subjects' correlation coefficients started at a very high level (0.88 ± 0.04). They showed a sharp rise in their correlation coefficients, reaching asymptotic levels (0.96 ± 0.01) significantly higher than their initial levels ($t(1)$ = -6.1, $p = 0.00008$).

### Retention

When the subjects were retested in Task A on the third day, their mean levels of performance were significantly higher than they had been when they first learned Task A on the second day (0.86 ± 0.04 vs. 0.83 ± 0.06; $t(11) = 4.1$, $p = 0.002$).

## Discussion

The subjects in this experiment demonstrated significant retention of Task A, even though they practiced an intervening Task B under the same circumstances that caused RI in Experiment 1a. There are several ways to account for this.

Maximum RI has been shown to occur when the second task is highly similar to the first in its stimuli and highly dissimilar in its required responses. Similarity between two tasks can occur along many different task dimensions, including the meaning of the learned verbal material [42], the type of memory task (for example, recognition versus recall tasks) [30], the modality of stimulus presentation [47], and the cognitive demands of the learned task [22]. RI is greatest when the nature of two tasks are similar across more than one of these dimensions [72]. It is possible that moving to the targets in the absence of perturbing forces is sufficiently dissimilar to Task A that RI is minimal or non-existent.

The fact that two tasks must be of a similar nature to cause RI suggests that RI depends on some degree of confusion betwen the tasks. What had been learned in Task A may be confused with what was learned in Task B. This confusion may occur either when Task B is learned or when Task A is recalled [11, 41, 43]. In either case, moving to the targets in the absence of forces was easy to recognize as a new task. This differentiability may explain the lack of RI in Experiment 1b.

It is interesting to note that subjects continued to display aftereffects for a number of targets, even though they knew that the forces had been turned off. This observation suggests a certain cognitive impenetrability in the motor system. The continuation of the aftereffects not likely due to the slow decay of a peripheral adaptation to the task, equivalent to visual afterimages. Unpublished data from our lab have shown that subjects will often displayed aftereffects for their first few movements when they returned to the manipulandum after a 24 hour break, even though they were told that the forces would not be on.

In some of the earliest related work using a learning paradigm that included a motor component, Siipola [59] proposed a plausible explanation of the NT. She employed a task in which subjects had to move a lever to a location indicated by a set of visual stimuli. Once subjects had learned the proper responses for one such set of stimuli, they were then asked to make different responses to the same stimuli. In this second task, subjects were found to make frequent errors in which they moved in the direction of the first set of responses learned. Siipola termed these "reversion errors," since the subjects reverted to an earlier response. The reversion errors were frequently only partial, in that subjects did not often move all the way to the inappropriate target. Instead, subjects would begin in the wrong direction and would correct themselves at some point during the movement.

As Siipola pointed out, one advantage in studying NT in motor tasks is that partial reversion errors can be detected more easily in a movement than in a verbal response. In fact, Melton and Irwin studied the phenomenon of reversion errors (also known as "intrusions") in a task of verbal learning [43]. These authors concluded that overt intrusions could not account for many of the errors that occur when subjects learn two different lists of words.

The continuing aftereffects displayed by the subjects in Task B can be considered to be reversion errors. Their movements indicated that they were compensating for the forces they had learned in Task A. If the forces in Task A had pushed a subject to the left, for example, that subject's reversion errors deviated to the right.

# Experiment 2

## Introduction

The influence of time on RI has been been explored in a number of learning paradigms, with humans and animals [39, 61, 67, 71]. One general rule to emerge from these studies is that RI decreases as the time between original learning and the disrupting stimulus increases. Although most of this work has been conducted in non-humans, the earliest known report of retrograde interference came from a study in humans [46] (cited in [72]). In this report on the learning of nonsense syllables, the ability of an intervening task to induce RI diminished if it was learned after as few as 6 minutes had passed since the time of original learning. The authors proposed that the original learning underwent a process of consolidation in which it became less vulnerable to disruption. The goal of Experiment 2 was to investigate the influence of time on RI in a motor learning task.

## Method

### Subjects

Naive volunteers (n = 24; male/female: 8/4) were drawn from the MIT community. Subjects classified themselves as right-handed and reported that they did not have any neurological disorders. Subjects were between the ages of 18 and 35, with a mean age of 24.0 years and a standard deviation of ± 4.8 years.

The apparatus and measurements were identical to those used in Experiments 1a and 1b. The procedure was nearly identical to that in Experiments 1a and 1b and so will be described only briefly here.

### Procedure

Subjects were divided into 2 groups, Group 1 (n = 12; male/female: 8/4) and Group 2 (n = 12; male/female: 8/4). Subjects in both groups were tested over 3 days. On the first day, they engaged in a period of initial practice, after which they performed in the baseline task. On the second day, subjects learned to move the manipulandum for one target set. The manipulandum produced perturbing forces (Task A). Both groups were then dismissed. Group 1 returned 4 hours later and Group 2 returned 8 hours later, at which time they engaged in an interfering Task B for one target set. Subjects did not engage in a set of 50 warm-up movements with no forces before learning Task B. Task B consisted of moving the manipulandum to one set of targets with no perturbing forces. Following Task B, the subjects were dismissed for the day. On the third day, subjects were retested for one target set in Task A.

## Results

Using the mean value of the correlation coefficients as the measure of performance in each target set, there was no difference in performance in any of the conditions between Groups 1 and 2 (**Task A:** 0.82 ± 0.06 vs. 0.84 ± 0.04; $t(19) = -1.1$, $p = 0.29$; **Task B:** 0.80 ± 0.06 vs. 0.81 ± 0.05; $t(19) = -0.42$, $p = 0.68$; **retest in Task A:** 0.85 ± 0.04 vs. 0.87 ± 0.04; $t(19) = -1.0$, p = 0.32). The two groups will therefore be combined and will be considered together.

### Task A

The performance in Task A was very similar to that of the previous groups of subjects, and so will be presented very briefly. Subjects improved significantly during the one target set in Task A 3-5. This improvement was not seen in the 180° probe targets.

### Task B

Subjects' mean performance in Task B was significantly less than in Task A (0.81 ± 0.05 vs. 0.83 ± 0.05; $t(20) = 2.4$, $p = 0.026$).

### Retention

When retested in Task A on day 3, subjects showed a significantly better performance than they had on day 2 (0.86 ± 0.04 vs. 0.83 ± 0.05; $t(20) = 3.6$, $p = 0.0016$).

### Correlation between NT and RI

A plot of retention of Task A as a function of the amount of NT demonstrates that the amount of NT a subject experiences is a strong predictor of the amount of RI that subject will experience (Fig. 3-9 $r^2 = 0.50$, $F(1,19) = 19.16$, $p = 0.0003$).

## Discussion

**Retention** These results demonstrate that there is significant retention of Task A if as few as 4 hours elapse before an interfering Task B was learned. This contrasts with the lack of retention if subjects learned Task B immediately after Task A. In the next section, the results from Experiments 1a, 1b, and 2 will be compared directly with each other. This will provide an overall view of the factors that influence retention and RI.

**NT** When these subjects learned Task B, their performance was not as high as it had been in Task A. Two facts should be born in mind, however. First, subjects did not receive any warm-up practice before Task B. Each day before Task A, subjects engaged in a series of warm-up movements to 50 targets with no perturbing forces. These warm-ups were necessary to refamiliarize subjects with the precise timing of the task. In order to compare the effect on retention of learning Task B immediately after Task A to its effect if 4 or 8 hours elapsed, it was important not to introduce any additional differences besides the amount of time that had passed. If the subjects in Experiment 2 had been allowed to move to 50 targets without forces before learning Task B, it would have complicated the conclusions that could have been drawn about the influence of time. By allowing warm-up before Task A and not before Task B, however, measures of performance are not as comparable as they would otherwise be.

Warm-up activities have been shown to enhance performance in verbal [25, 66] and motor studies [5, 28]. Second, as will be shown in the following analysis, the amount of NT after a 4 or 8 hour break was significantly less than that in Experiment 1a.

**Relation between RI and NT** The strong correlation between the amount of NT and the retention, or lack of retention, of Task A suggests that there is a common mechanism responsible for both NT and RI. One candidate for this common mechanism is suggested by the reversion errors presented earlier. When switched to Task B, subjects persisted in producing responses learned in Task A. It is quite likely, therefore, that subjects did not successfully identify Task B as a separate task from Task A. Under this interpretation, the extent to which subjects classified the two tasks as separate determined the extent of interaction between the tasks. NT would have resulted from a persistance of previously learned responses, and RI would have resulted when the learning that does occur in Task B replaces the previous learning in Task A. It is interesting to note in this context that computational studies have suggested that one function of consolidation is to facilitate task segregation. O'Reilly and McClelland [48] demonstrated that the gradual incorporation of new learning can significantly reduce RI (referred to in the computational literature as catastrophic interference).

# Analysis of Results from Experiments 1a, 1b, and 2

## Introduction

In this section, results from the previous 3 experiments will be compared in order to gain an understanding of the variable that affect transfer and retention of motor learning. The comparisons will be concerned with the effect of time on NT and the effects of time and the nature of the intervening task on RI. A schematic summary of the treatment conditions of these groups can be found in Fig. 3-10.

**Time and NT** The subjects in Experiment 1a, who learned Task B immediately after Task A, demonstrated significantly more NT than the subjects in Experiment 2, who waited either 4 or 8 hours between learning Task A and learning Task B (-0.06 ± 0.03 vs. -0.02 ± 0.04; $t(30) = 2.5$, $p = 0.018$; Fig. 3-6). The amount of NT was defined as the difference between mean performance in Task B and mean performance in Task A.

**Time, Task, and RI** A comparison between the retention of Task A from day 2 to day 3 was made between subjects in Experiments 1a (Groups 1 and 2), 1b, and 2. This allowed an assessment of the relative effects of various time intervals and two different intervening tasks on the ability of subjects to retain their motor skill in Task A. Retention was measured as the difference in mean performance in Task A on day 2 and day 3. A one-way analysis of variance (ANOVA) revealed a significant difference in the retention of Task A among the 4 groups ($F(3,52) = 3.41$, $p = 0.024$; Fig. 3-8). Uncorrected post-hoc pairwise comparisons revealed a significant difference between the amount of retention in Group 1 and Group 2 from Experiment 1a (0.043 vs. 0.005; $t(52) = 3.1$ $p < 0.005$).[2] The subjects in Experiment 1b also retained significantly more of Task A than Group 2 from Experiment 1a (0.031 vs. 0.005; $t(52) = 2.5$, $p < 0.02$), as did the subjects in Experiment 2 (0.027 vs. 0.005; $t(52) = 2.1$, $p < 0.05$). However, if a Bonferroni correction is made for the fact that there were 6 possible post-hoc comparisons, the only significant difference that remained was between the amount of retention in Group 1 and Group 2 from Experiment 1a .

## General Discussion

These results provide the first evidence that human motor memories are transformed with the passage of time from an initial fragile state to a later, more solid state. This consolidation occured rapidly – in as little as 4 hours. It is interesting to note that the

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[2] The degrees of freedom for the pairwise comparisons was based on the degrees of freedom for the best estimate of the population variance: the mean-square error within the 4 groups in the ANOVA [37].

memory consolidated without the need for sleep. The initial state of motor memory is not only vulnerable to being lost by subsequent learning (RI), it is also capable of interfering with the performance of a susequent task (NT). Thus, early motor memories can be distinguished from consolidated motor memories on two counts.

Several possibilities exist to account for this consolidation. They fall under two broad categories: biochemical consolidation and anatomical consolidation. Experiments using protein synthesis inhibitors have suggested that gene expression is a necessary step for the long-term storage of learning [67, 17]. It has also been proposed that the protein-dependent, long-term memories are more resistant to disruption than short-term memories [67, 62, 52]. The time course of experience-dependent gene expression is also consistent with the time course of my results [9].

Studies of patients with localized cerebral lesions have suggested that consolidation can occur as a result a change in the anatomical locus of a memory trace [44, 45, 63]. This anatomical consolidation, however, appears to take place over a much longer time scale than I observe in my subjects. While there have been no studies showing that anatomical consolidation can occur merely with the passage of a short amount of time, recent electrophysiological and neuroimaging studies showing that practice can result in a shift in the areas of neural activation within a single practice session or block of sessions [65, 23]. These latter studies, however, have not shown that the shift in the locus of neural activation is accompanied by a resistance to RI.

Most studies of consolidation in humans have concerned themselves with explicit learning tasks [61]. Reports of consolidation in perceptual learning, a form of implicit learning, use the term to refer to a necessary period of practice-free improvement in a skill [33], which is a different phenomenon than that described in the explicit learning literature and in my motor learning task. By demonstrating a common principle in explicit and implicit learning tasks, the results presented here suggest the intriguing possibility that two distinct learning systems may share common mechanisms of encoding and storing new experiences.

# Figures

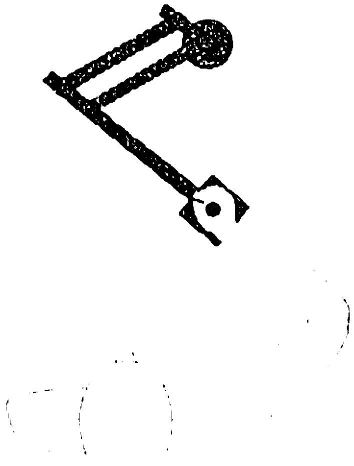

Figure 3-1: **The experimental setup.** The two-link planar manipulandum was equipped with two motors that could deliver torques independently to either of the the two joints of the manipulandum.

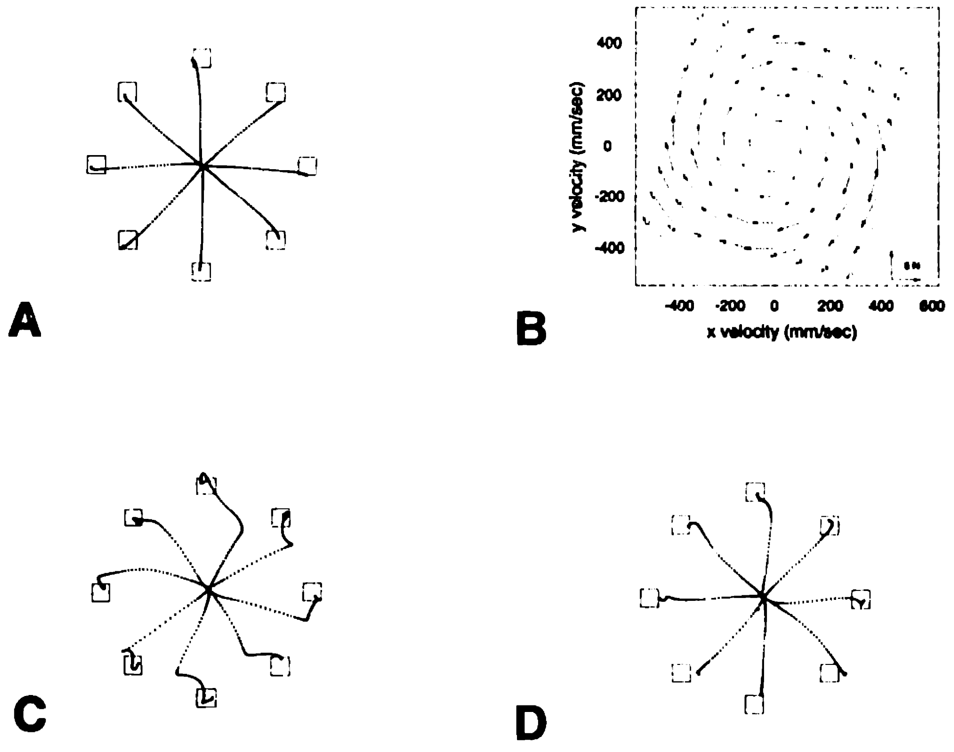

Figure 3-2: **Trajectories from one subject illustrating the stages of the experiment. A:** Typical baseline trajectories for this subject. For ease in displaying the trajectories, a movement towards the center target from one of the outward targets is plotted as if it were a movement out from the center. For example, a movement to the center from the upward target is displayed as if it were a movement from the center downward. **B:** The clockwise (B) and velocity-dependent forces used in this study. The forces are plotted in velocity space. The direction and length of an arrow indicate the direction and magnitude of the forces at that location in velocity space. For example, when subjects were not moving, i.e., when they were at zero x-velocity and zero y-velocity, the handle produced no forces. **C:** When the forces were first turned on, the subject's hand was perturbed from his baseline trajectories. **D:** The subject's movements in the presence of the forces after approximately 5 minutes of practice. After the subject practiced moving in the presence of the forces, he was able once again to move in a straight line to the targets. The correlation between a subject's trajectories in the presence of the forces and that subject's baseline trajectories provides a measure of the extent to which that subject has learned to compensate for the forces. For example, the trajectories pictured in (C) had a mean correlation of 0.66 when compared to the baseline trajectories in (A). After 5 minutes of practice, the subject's trajectories (D) had acheived a mean correlation of 0.91.

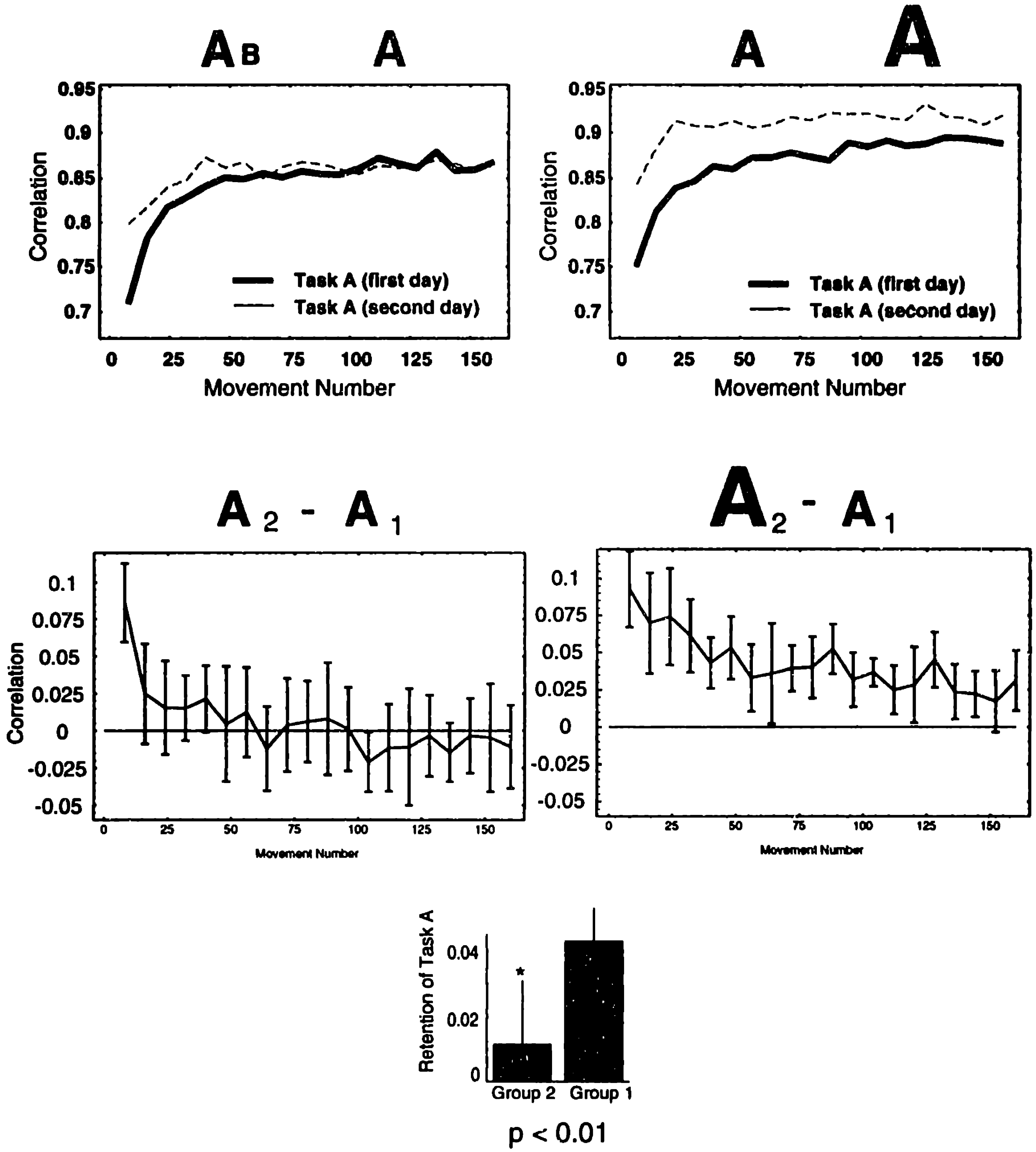

Figure 3-3: **The graphs on the right show the retention of motor learning in Group 1.** These subjects learned Task A on Day 2 (solid, dark curve) and then returned 24 hours later and were re-tested in the same task (light, dashed curve). The difference in their performance on Day 2 and Day 3, along with 95 % confidence intervals is shown in the lower right graph. The graphs on the left show the lack of significant retention in Group 2. Subjects in Group 2 learned an intervening Task B (performance in Task B shown in Fig. 3-4) immediately after first learning Task A. When re-tested in Task A on Day 3 (light, dashed line), these subjects performed, on average, no better than on Day 2 (dark, solid line). The bar chart shows the amount of retention for the two groups. Graphs are labelled according to the conventions in Fig. 3-10.

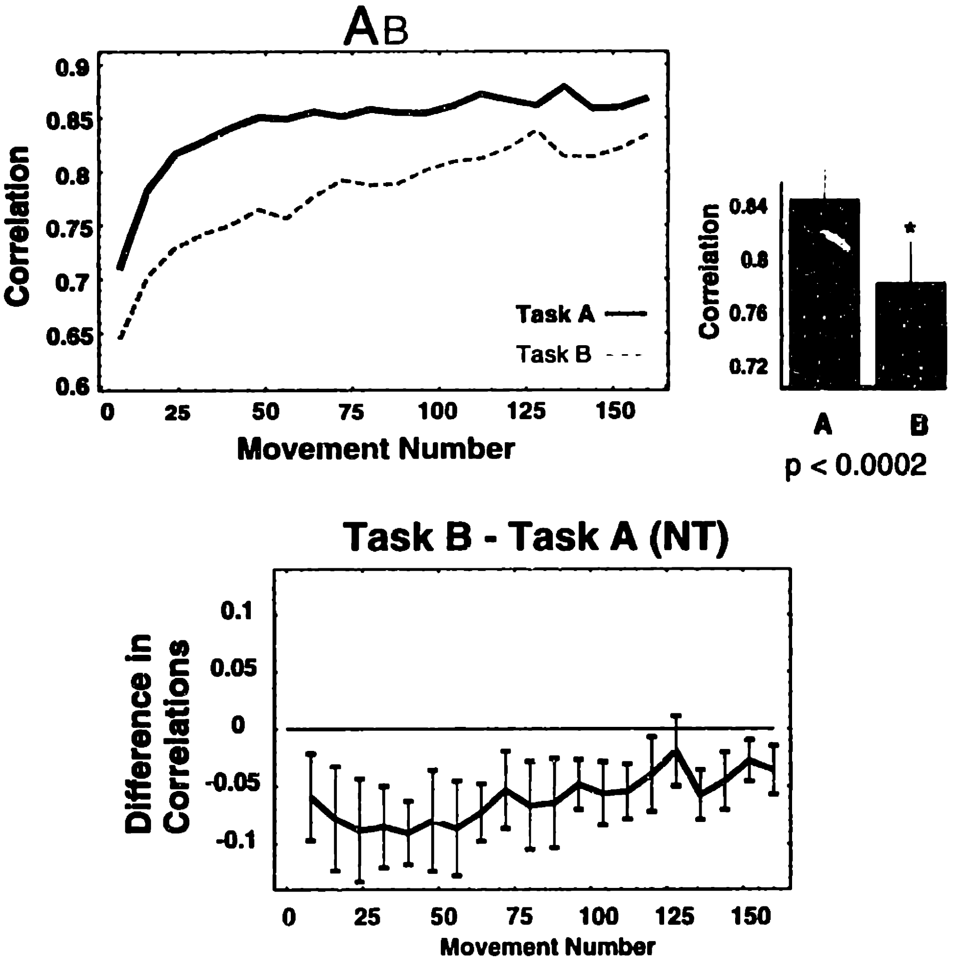

Figure 3-4: **Learning curves demonstrating NT in Group 2.** Each curve depicts the mean of the learning curves for 11 subjects. Each point on the curve is the average of eight correlations, one in each of the target directions. In the upper graph, the dark, solid curve depicts the performance of the subjects in the first field, or Task A. The light, dashed curve represents the performance of these same subjects when they tried to learn a second field, Task B, immediately after the first field. The bar chart indicates that mean level of performance in Task B is significantly lower than that for Task A ($p < 0.0002$ paired t-test). The lower graph plots the difference and 95 % confidence intervals between the learning curves in Task A and Task B.

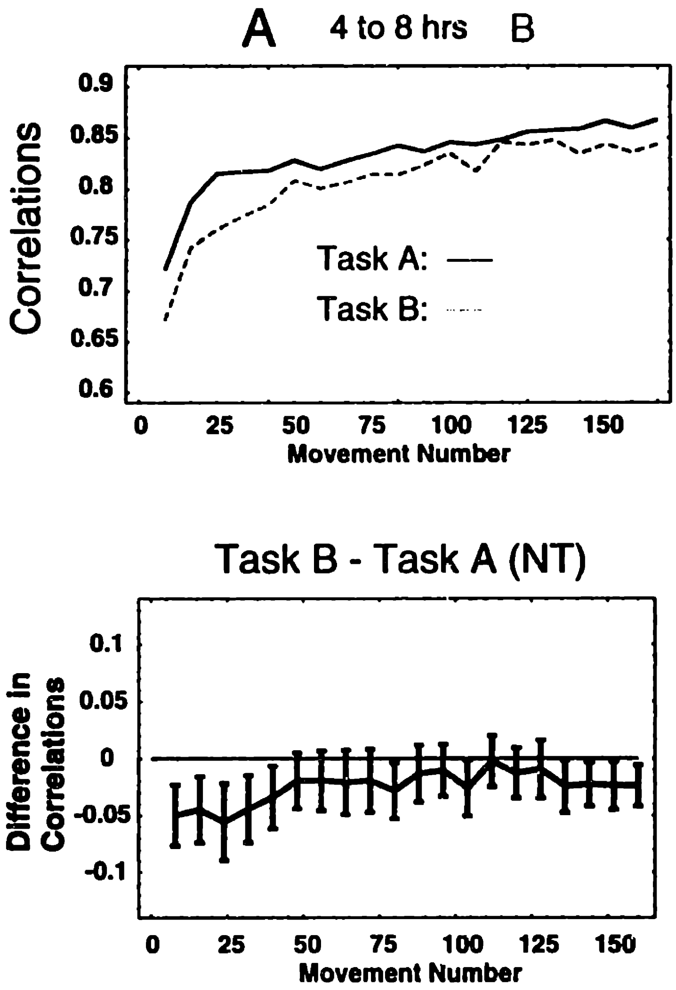

Figure 3-5: **Learning curves demonstrating reduced NT in Experiment 2.** Each curve depicts the mean of the learning curves for 21 subjects. Each point on the curve is the average of eight correlations, one in each of the target directions. In the upper graph, the dark, solid curve depicts the performance of the subjects in the first field, or Task A. The light, dashed curve represents the performance of these same subjects when they tried to learn a second field, Task B, either 4 or 8 hours after the first field. The lower graph plots the difference and 95 % confidence intervals between the learning curves in Task A and Task B.

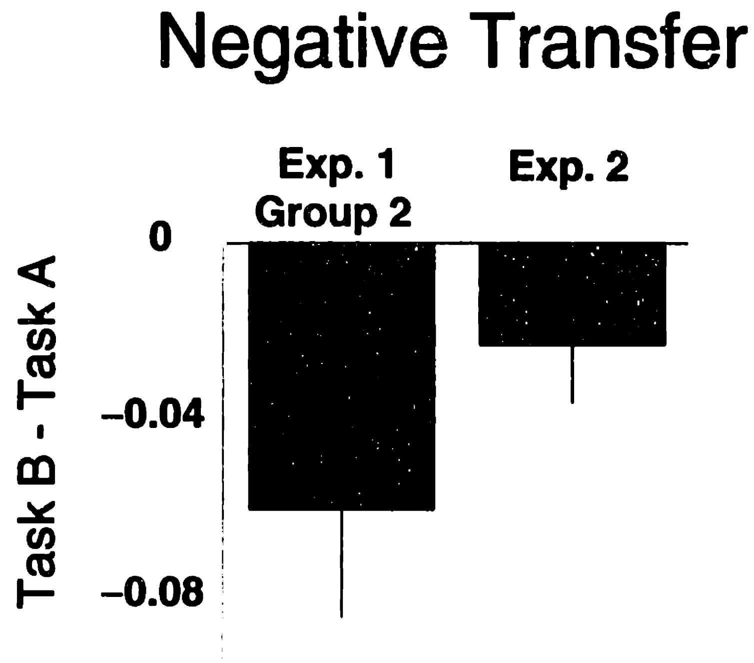

Figure 3-6: **NT for Experiment 1, Group 2 and Experiment 2.** In Experiment 1, Group 2 learned Task B immediately after Task A, whereas either 4 or 8 hours passed between the time subjects in Experiment 2 learned Task A and Task B. There is a significant difference between the amount of NT in these two groups (paired t-test, $p < 0.02$).

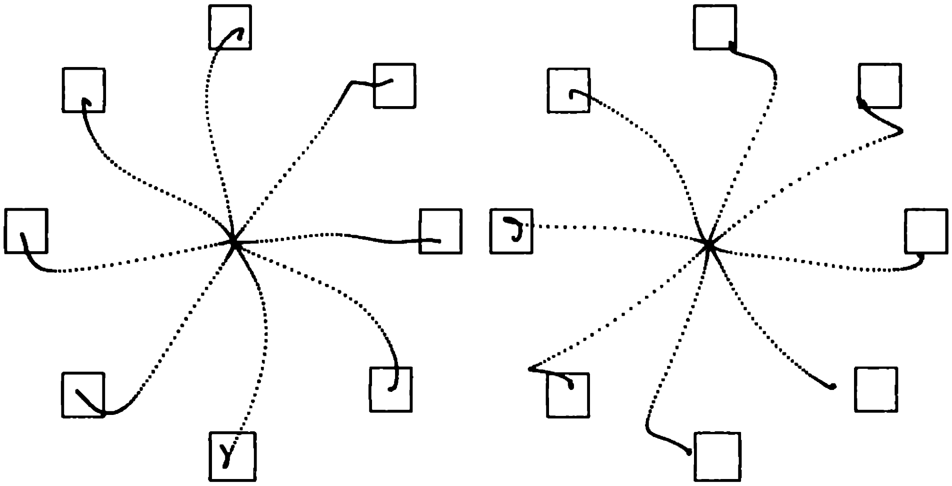

Figure 3-7: **The reversion errors on the first movement in each of the 8 target directions for two different subjects.** The subjects whose movements are depicted on the left had learned a clockwise curl field. The one on the right had learned a counterclockwise curl field. The curvature of the two trajectories indicates that the subjects produced torques to compensate for the force field they had been exposed to in Task A.

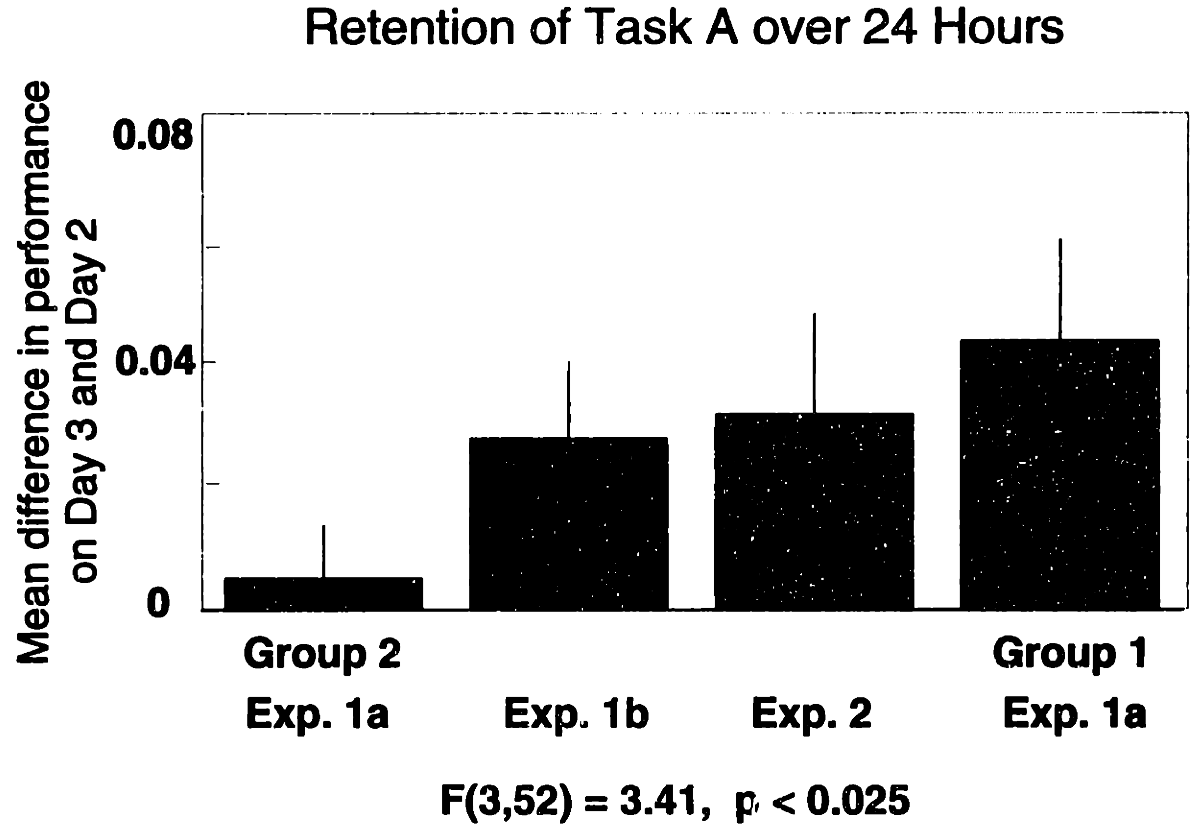

Figure 3-8: **Bar chart showing the amount of retention in each of the groups, as measured by the difference in mean performance on Day 3 and Day 2.** There is a significant difference between the amount of retention displayed by the 4 groups ($F(3,52) = 3.41$, $p < 0.025$). See text for details.

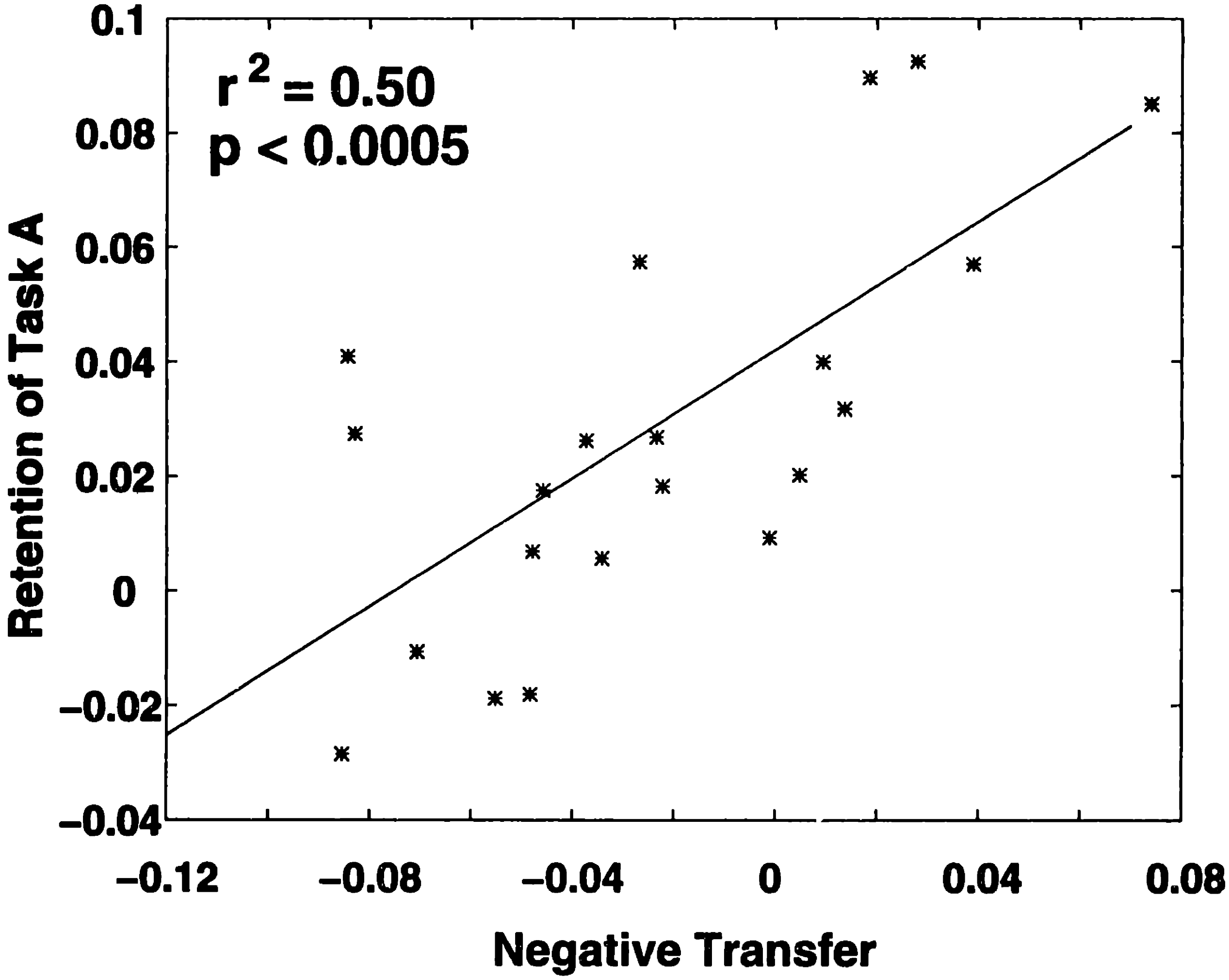

Figure 3-9: **Plot of amount of retention of Task A as a function of the amount of NT.** Magnitude of NT is a good predictor of the amount of RI.

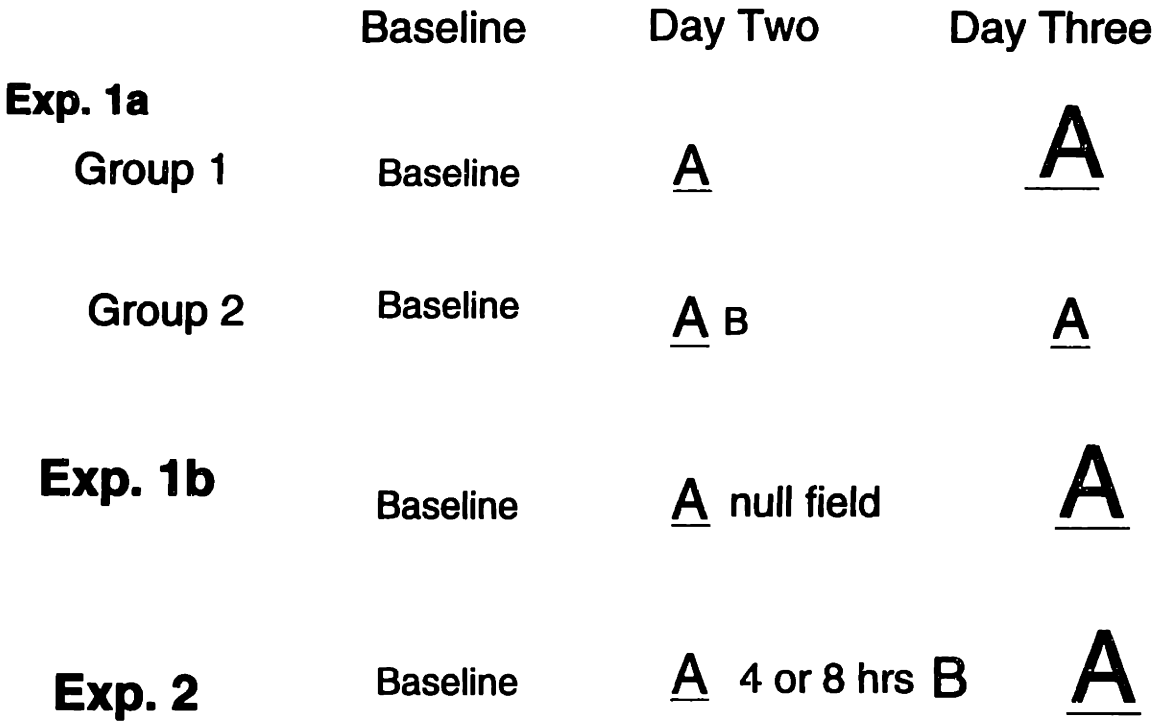

Figure 3-10: **A table depicting the treatment protocols of the 4 groups of subjects.** Each letter "A" indicates that subjects learned Task A for one target set (192 targets, approximately 5 minutes) The letter "B" indicates that subjects learned Task B for one target set. See the text for an explanation of the different tasks. The size of the letters represents the level of skill subjects attained in each target set. The larger letters indicate superior performance.

# Bibliography

[1] J. Adams and S. Dijkstra. Short-term memory for motor responses. *Journal of Experimental Psychology*, 71(2):314–318, 1966.

[2] J. A. Adams and S. Dijkstra. Short-term memory for motor responses. *Journal of Experimental Psychology*, 71:314–318, 1966.

[3] B. Agranoff, R. Davis, and J. Brink. Chemical studies on memory fixation in goldfish. *Brain Research*, 1:303–309, 1966.

[4] P. Alvarez, S. Zola-Morgan, and L Squire. The animal model of human amnesia: Long-term memory impaired and short-term memory intact. *Proceeding of the National Academy of Sciences*, 91:5637–5641, 1994.

[5] R. B. Ammons. Acquisition of motor skill. ii. rotary pursuit performance with continuous practice before and after a single rest. *Journal of Experimental Psychology*, 37:393–411, 1947.

[6] R. C. Atkinson and R. M. Shiffrin. Human memory: A proposed system and its control processes. In K. W. Spence, editor, *The Psychology of Learning and Motivation: Advances in Research and Theory*, pages 89–195. Academic Press, New York, N. Y., 1968.

[7] A. Baddeley. *Working Memory.* Oxford University Press, Oxford, 1986.

[8] A. Baddeley. *Human Memory: Theory and Practice.* Simon and Schuster, Inc., Needham Heights, MA, 1990.

[9] C. Bailey and E. Kandel. Molecular and structural mechanisms underlying long-term memory. In M. Gazzaniga, editor, *The Cognitive Neurosciences*, pages 19–36. The MIT Press, Cambridge, MA, 1995.

[10] K. E. Baker, R. C. Wylie, and R. M. Gagne. The effects of an interfering task on the learning of a complex motor skill. *Journal of Experimental Psychology*, 41(1):1–9, 1951.

[11] J. M. Barnes and B. J. Underwood. Fate of first-list associations in transfer theory. *Journal of Experimental Psychology*, 58:97–105, 1959.

[12] T. Brashers-Krug, R. Shadmehr, and E. Todorov. Catastrophic interference in human motor learning. In *Advances in Neural Information Processing Systems*, volume 7, 1995.

[13] G. E. Briggs. Retroactive inhibition as a function of the degree of original and interpolated learning. *Journal of Experimental Psychology*, 53:60–67, 1957.

[14] W. R. Bruce. Conditions of transfer of training. *Journal of Experimental Psychology*, 16(3):343–361, 1933.

[15] S. Corkin. Acquisition of motor skill after bilateral medial temporal-lobe excision. *Neuropsychologia*, 6:255–265, 1968.

[16] I. C. Faye. An impedance controlled manipulandum for human movement studies. S.m. thesis, MIT, 1986.

[17] J. Flexner, L. Flexner, and E. Stellar. Memory in mice is affected by intracerebral puromycin. *Science*, 141:57–59, 1983.

[18] R. French. Dynamically constraining connectionist networks to produce distributed, orthogonal representations to reduce catastrophic interference. In *Proceedings of the 16th Annual Conference of the Cognitive Science Society*, volume 16, pages 335–340, 1994.

[19] R. M. Gagne and H. Foster. Transfer of training from practice on components in a motor skill. *Journal of Experimental Psychology*, 39:47–68, 1949.

[20] M. Gazzaniga, editor. *The Cognitive Neurosciences.* The MIT Press, Cambridge, MA, 1995.

[21] E. J. Gibson. Retroactive inhibition as a function of degree of generalization between tasks. *Journal of Experimental Psychology*, 28:93–115, 1941.

[22] E. J. Gibson and J. J. Gibson. Retention and the interpolated task. *American Journal of Psychology*, 46:603-610, 1934.

[23] S Grafton, J Mazziotta, S Presty, K Friston, R Frackowiak, and M Phelps. Functional anatomy of human procedural learning determined with regional cerebral blood flow and pet. *Journal of Neuroscience*, 12:2542–2548, 1992.

[24] H. Gulliksen. Transfer of response in human subjects. *Journal of Experimental Psychology*, 15:496–516, 1932.

[25] C. E. Hamilton. The relationship between lenght of interval separating two learning tasks and performance on the second task. *Journal of Experimental Psychology*, 40:613–621, 1950.

[26] R. J. Hamilton. Retroactive facilitation as a function of degree of generalization between tasks. *Journal of Experimental Psychology*, 32(5):363–376, 1943.

[27] R. Held. Adaptation to rearrangement and visual-spatial aftereffects. *Psychologische Beitrage*, 6:439–450, 1962.

[28] A. L. Irion. Historical introduction. In E. A. Bilodeau, editor, *Principles of Skill Acquisition.* Academic Press, New York, NY, 1969.

[29] L. L. Jacoby and D. Witherspoon. Remembering without awareness. *Candian Journal of Psychology*, 36:300–324, 1982.

[30] J. Jenkins and I. Postman. An experimental analysis of set in rote learning. retroactive inhibition as a function of changing set. *Journal of Experimental Psychology*, 39:69–72, 1949.

[31] M. Jordan and J. Jacobs. Learning piecewise control strategies in a modular neural network architecture. In *IEEE Transactions on Systems, Man and Cybernetics*, volume 23, pages 337–345, 1993.

[32] J. Kaas. Plasticity of sensory and motor maps in adult mammals. In *Annual Review of Neuroscience*, pages 137–167. Society for Neuroscience, 1992.

[33] A. Karni and D. Sagi. The time course of learning a visual skill. *Nature*, 365(6443):250–2, 1993.

[34] D. Lewis, D. McAllister, and J. Adams. Facilitation and interference in performance of the modified mashburn apparatus: I. the effects of varying the amount of original learning. *Journal of Experimental Psychology*, 41:247–260, 1951.

[35] D. Lewis, A. Shephard, and J. Adams. Evidences of associative interference in psychomotor performance. *Science*, 110:271–273, 1949.

[36] D. Lewis, P. N. Smith, and D. McAllister. Retroactive facilitations and interference in perfromance on the modified two-hand coordination task. *Journal of Experimental Psychology*, 44:247–260, 1952.

[37] G. R. Loftus and E. F. Loftus. *Essence of Statistics*. McGraw-Hill, New York, 1988.

[38] J. McGaugh and M. Herz. Current issues and memory consolidation. In James McGaugh and Michael Herz, editors, *Neurobiology of Learning and Memory*, pages 3–59. Albion Pub. Co., San Francisco, CA, 1972.

[39] J. McGaugh and M. Herz, editors. *Memory consolidation*. Albion Pub. Co., San Francisco, CA, 1972.

[40] J. L. McGaugh and H. P. Alpern. Effects of electroshock on memory: Amnesia without convulsions. *Science*, 152:665-666, 1966.

[41] J. A. McGeoch and A. L. Irion. *The Psychology of Human Learning.* Longmans Breen, New York, NY, 2nd edition, 1952.

[42] J. A. McGeoch and W. T. McDonald. Meaningful relation and retroactive inhibition. *American Journal of Psychology*, 43:579–588, 1931.

[43] A. W. Melton and J. M. Irwin. The influence of degree of interpolated learning on retroactive inhibition ond the overt transfer of specific responses. *American Journal of Psychology*, 53:173–203, 1940.

[44] B. Milner, S. Corkin, and H. L. Teuber. Further analysis of the hippocampal amnestic syndrome: 14 year follow-up of h.m. *Neuropsychologia*, 6:215–234, 1968.

[45] M. Mishkin. *Philosophical Transactions of the Royal Society of London B*, 298:85–92, 1982.

[46] G. E. Muller and A. Pilzecker. Experimentelle beitrage zur lehre vom gedachtniss. *Z. Psychol.*, pages 1–300, 1900.

[47] J. W. Nagge. An experimental test of the theory of associative interference. *Journal of Experimental Psychology*, 18:663–682, 1935.

[48] R. C. O'Reilly and J. L McClelland. Hippocampal conjunctive encoding, storage and recall: Avoiding a tradeoff. Technical report, Carnegie Mellon University, 1994.

[49] C. E. Osgood. The similarity paradox in human learning: a resolution. *Psycological Review*, 56:132–143, 1949.

[50] M. I. Posner and A. E. Konick. On the role of interference in short-term retention. *Journal of Experimental Psychology*, 72:221–231, 1966.

[51] E. S. Robinson. The similarity factor in retroaction. *American Journal of Psychology*, 39:297–312, 1927.

[52] M. Rosenqweig and E. Bennett. Direct processes and modulatory influences in the stages of memory formation. In J. McGaugh and M. Herz, editors, *Neurobiology of Learning and Memory*, pages 263-288. Guilford Press, New York, NY, 1984.

[53] D. Schacter and E. Tulving. *Memory Systems 1994*. MIT Press, Cambridge, MA, 1994.

[54] D. L. Schacter. Implicit memory: History and current status. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 13:501–518, 1987.

[55] D. L. Schacter, Chiu C. Y. P., and Ochsner K. N. Implicit memory: a selective review. *Annual Review of Neuroscience*, 16:159–182, 1993.

[56] R. Schmidt. *Motor Control and Learning: A Behavioral Emphasis.* Human Kinetics, Champaign, IL, 2nd edition, 1988.

[57] R. Shadmehr and F. Mussa-Ivaldi. Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience*, 14(5):3208–3224, 1994.

[58] J. B. Shea and D. L. Wright. When forgetting benefits motor retention. *Research Quarterly for Exercise and Sport*, 62(3):293–301, 1990.

[59] E. Siipola. Implicit or partial reversion-errors: a technique of measurement and its relation to other measures of transfer. *Journal of Experimental Psychology*, 26:53–73, 1940.

[60] E. Siipola and H. E. Israel. Habit-interference as dependent upon stage of training. *Journal of Psychology*, 45(2):205–227, 1933.

[61] L. Squire and P. Alvarez. Retrograde amnesia and memory consolidation: a neurobiological perspective. *Current Opinion in Neurobiology*, in press.

[62] L. Squire, L. Davis, and C. Spanis. Neurobiology of amnesia. *Science*, 209:836–837, 1980.

[63] L. Squire and S. Zola-Morgan. In J Deutsch, editor, *The Physiological Basis of Memory*, pages 199–268. Academic, New York, NY, 1983.

[64] L. R. Squire. Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience*, 99:195–231, 1992.

[65] J Tanji and K Shima. Role for supplementary motor area cells in planning several movements ahead. *Nature*, 371(6496):413–416, 1994.

[66] L. E. Thune. The effect of different types of preliminary activities on subsequent learning of paired-associate material. *Journal of Experimental Psychology*, 40:423–438, 1950.

[67] T. Tully. Genetic dissection of consolidated memory in drosophila. *Cell*, 79(1):35–47, 1994.

[68] B. J. Underwood. The effect of successive interpolations on retroactive and proactive inhibition. *Psychological Monographs*, 59(3):1–33, 1945.

[69] B. J. Underwood. Tertroactive and proactive inhibition after five and forty-eight hours. *Journal of Experimental Psychology*, 38:29–38, 1948.

[70] B. J. Underwood. Proactive inhibition as a function of time and degree of prior learning. *Journal of Experimental Psychology*, 39:24–34, 1949.

[71] H. Weingartner and E. Parker, editors. *Memory consolidation: psychobiology of cognition.* L. Erlbaum Associates, Hillsdale, N.J., 1984.

[72] Woodworth and Schlosberg. *Experimental Psychology.* Holt and Company, New York, NY, 1958.

[73] K. S. Yum. An experimental test of the law of assimilation. *Journal of Experimental Psychology*, 14:68–82, 1931.

[74] S. Zola-Morgan and L. Squire. The primate hippocampal formation: Evidence for a time-limited role in memory storage. *Science*, 250:288–290, 1990.