

Multiple Motor Learning Experiences Enhance Motor Adaptability

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Abstract

■ Traditional motor learning theory emphasizes that skill learning is specific to the context and task performed. Recent data suggest, however, that subjects exposed to a variety of motor learning paradigms may be able to acquire general, transferable knowledge about skill learning processes. I tested this idea by having subjects learn five different motor tasks, three that were similar to each other and two that were not related. A group of experimental subjects first performed a joystick-aiming task requiring adaptation to three different visuomotor rotations, with a return to the null conditions between each exposure. They then performed the same joystick-aiming task but had to adapt to a change in display gain instead of rotation. Lastly, the subjects used the joystick-aiming task to learn a repeating sequence of movements. Two

groups of control subjects performed the same number of trials, but learned only the gain change or the movement sequence. Experimental subjects showed generalization of learning across the three visuomotor rotations. Experimental subjects also exhibited transfer of learning ability to the gain change and the movement sequence, resulting in faster learning than that seen in the control subjects. However, transient perturbations affected the movements of the experimental subjects to a greater extent than those of the control subjects. These data demonstrate that humans can acquire a general enhancement in motor skill learning capacity through experience, but it comes with a cost. Although movement becomes more adaptable following multiple learning experiences, it also becomes less stable to external perturbation. ■

INTRODUCTION

The ability to adaptively and flexibly modify motor behavior is a key component contributing to the varied repertoire of skilled actions seen in everyday human behavior. The capacity to generalize new behaviors from previously acquired ones has been well studied (cf. Abeele & Bock, 2001a; Welch, Briegeman, Anand, & Browman, 1993; Lee, Swanson, & Hall, 1991; McCracken & Stelmach, 1977). This ability to interpolate new motor solutions based on prior experience seems to be limited to actions that have relatively similar requirements (cf. Abeele & Bock, 2001a, 2001b; Thoroughman & Shadmehr, 2000). In fact, there is much evidence supporting the specificity of learning principle, which suggests that what subjects learn is specific to the learning context and the task performed (Bachman, 1961) and that generalized motor abilities do not exist (Henry, 1960, 1961). Bachman (1961) demonstrated that the rate of learning two similar balancing tasks, balancing on a stabilometer platform and climbing a freestanding ladder, were virtually uncorrelated across subjects. In contradiction to this specificity of learning principle, recent evidence suggests that a facilitation of learning can be observed when subjects transfer to a new skill

that is independent from those recently experienced, if they first participate in multiple bouts of learning (Bock, Schneider, & Bloomberg, 2001; Roller, Cohen, Kimball, & Bloomberg, 2001). For example, Roller et al. (2001) found that subjects that had first adapted throwing movements while wearing altered visual gain lenses (minifying and magnifying) and up-down reversing lenses exhibited an enhanced capacity for future adaptation to prism wedge lenses. That is, plasticity was enhanced by the prior adaptation experiences. The authors suggested that the subjects had acquired a general improvement in associative learning.

The mechanisms behind this learning to learn are unclear. One possibility is that there may have been a potentiation of the underlying neural circuitry supporting the behavior. Learning new visuomotor mappings involves activation of posterior parietal regions, regardless of whether the adaptive stimulus is rotated visual feedback or a visual shift induced with prism wedges (Ghilardi et al., 2000; Inoue et al., 1997, 2000; Clower et al., 1996). The previously reported facilitation of learning (Bock et al., 2001; Roller et al., 2001) may therefore have been mediated by prior potentiation of the neural circuitry in these parietal regions, since all of the tasks studied required visuomotor adaptation. There is substantial evidence that both cortical and synaptic plasticity occur during learning (for a review, see Buonomano &

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Merzenich, 1998) and that such plasticity is localized to the neural regions mediating the learned behavior (Kleim et al., 2002).

It is currently unclear whether this phenomenon extends to different types of learning as well. Specifically, it is not known whether multiple visuomotor adaptation experiences would result in enhanced sequence learning, since this process is both neurally and strategically different from visuomotor adaptation. Thus, one purpose of these experiments was to determine whether adaptation to multiple visuomotor distortions would enhance both the adaptation to a new visuomotor distortion and the acquisition of a movement sequence.

It is somewhat surprising that enhanced plasticity would need to be drawn out through experience with multiple learning exposures and that subjects are not always capable of their maximum rate of learning. Previous work demonstrates that both facilitation and interference of learning, once invoked, will remain for a period of at least 1 month (Bock et al., 2001; Roller et al., 2001). It is unclear then why people are not always in this state of accelerated learning. This finding suggests that the learning enhancement is associated with some behavioral cost. We propose that one such cost may be movement stability. Intertrial movement instability may be beneficial during learning, as it would allow for modification of performance across trials. Under typical movement conditions, however, it is desirable to have a high degree of stereotypy in performance from trial to trial, as this allows for predictable movement control. Therefore, an additional purpose of these studies was to determine whether multiple motor learning experiences result in reduced movement stability in the face of transient perturbations.

RESULTS

Thirty-three subjects participated in this study. The multiple learning subject group (ML) learned five tasks over 2 days, with a return to the null conditions in between each learning experience. All five tasks were variants of a basic, center-out joystick-aiming task, with targets and real-time feedback of cursor movement presented to subjects on a computer monitor. Tasks 1–3 were visuomotor adaptation tasks in which the feedback display was rotated in the counterclockwise direction about the central start position by 15°, 30°, or 45°. These conditions were presented to the subjects in a counterbalanced order, with ML1 subjects learning first the 30° rotation, then 15°, followed by 45°. ML2 subjects learned first the 45° rotation, then 15°, followed by 30°. In Task 4, subjects adapted movements to an increased gain of display. For Task 5, they learned a repeating sequence of movements. Control subjects experienced the same number of trials with the joystick device and the display, but only learned either Task 4

(gain learning group, GL) or 5 (sequence learning group, SL).

Subjects Exhibit Generalization of Learning across the Three Visuomotor Rotations

Figure 1 presents initial endpoint error (IEE) for the ML1 and ML2 subjects learning the first and the last of the three visuomotor rotations (error bars have been omitted from the graphs for clarity; group effect sizes are reported below). Subjects demonstrated an ability to generalize learning across the three visuomotor rotation tasks [Group × Trial interaction for 30° adaptation: $F(1,83) = 1.6, p < .01$; Group × Trial interaction for 45° adaptation, $F(1,25) = 4.4, p < .05$, group difference in quadratic trend across adaptation trials]. That is, subjects adapting to the 30° rotation after having previously experienced the 45° and the 15° rotations adapted

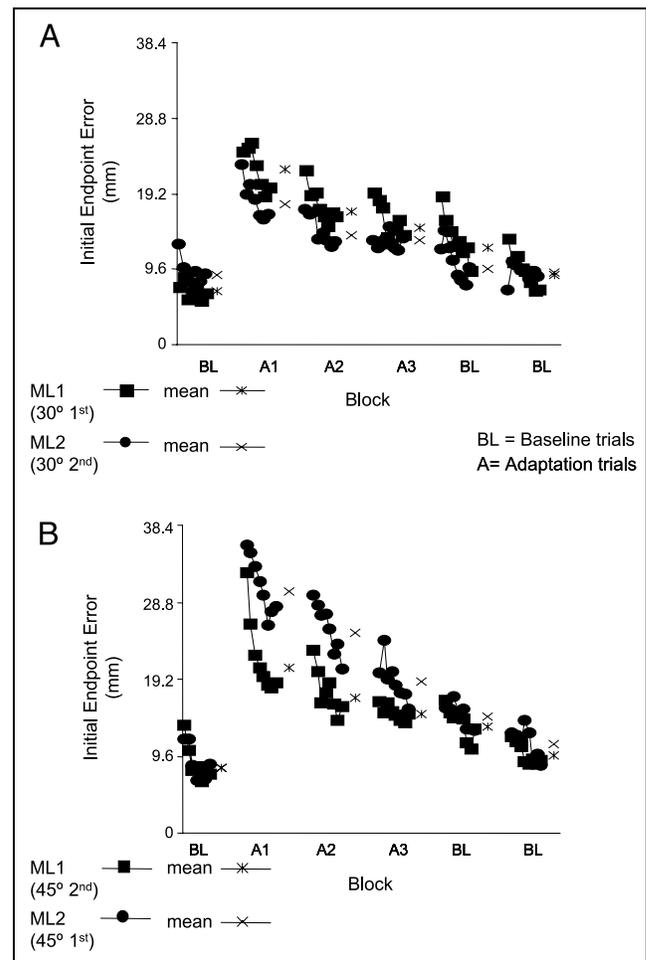


Figure 1. Generalization of learning among the three visuomotor rotations. (A) Adaptation to a 30° rotation. The subjects who have already adapted to 45° and 15° rotations learn more quickly. (B) Adaptation to a 45° rotation. As in (A), the experienced subjects adapt to the distortion more quickly. The first data point for each block reflects performance on the first trial, and subsequent data points are the mean over three trials.

more quickly than subjects adapting to the 30° rotation without any prior adaptation experience. This effect was enhanced for adaptation to a 45° rotation (for 30°, $p < .01$, $\omega^2 = .07$, medium effect size; for 45°, $p < .05$, $\omega^2 = .35$, large effect size). The group differences were largest during the first block of learning.

Prior Adaptation to Visuomotor Rotations Increases Rate of Adaptation to an Altered Gain of Display

The ML subjects (all subjects that adapted to the three visuomotor rotations, regardless of order of presentation) demonstrated a slight advantage over the GL subjects early in learning when adapting to the change in gain of display [Figure 2, group difference in quadratic trend across the trials, $F(1,25) = 4.3$, $p < .05$, $\omega^2 = .08$, medium effect size]. The GL subjects had the same number of trials of experience with the joystick device on Day 1, but did not adapt to any visuomotor rotations.

Prior Adaptation to Visuomotor Transformations Increases Rate of Sequence Learning

The ML subjects demonstrated faster sequence learning than the SL subjects [Figure 3, Group \times Block interaction, $F(8,120) = 3.7$, $p < .01$, $\omega^2 = .16$, large effect size]. The SL subjects had the same number of trials of experience with the joystick device as the ML subjects, but did not adapt to any visuomotor rotations or to the altered gain of display. The GL subjects performed movements to targets that were presented in a random order during these blocks. Their reaction time (RT) is plotted for comparison in Figure 3. Planned follow-up

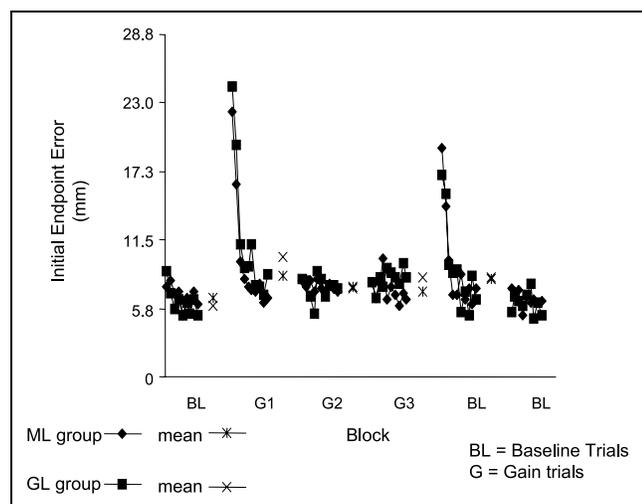


Figure 2. Facilitation of adapting to an altered gain of display. ML subjects are those that first adapted to the three visuomotor rotations. They are faster at gain adaptation than GL subjects. The first data point for each block reflects performance on the first trial, and subsequent data points are the mean over three trials.

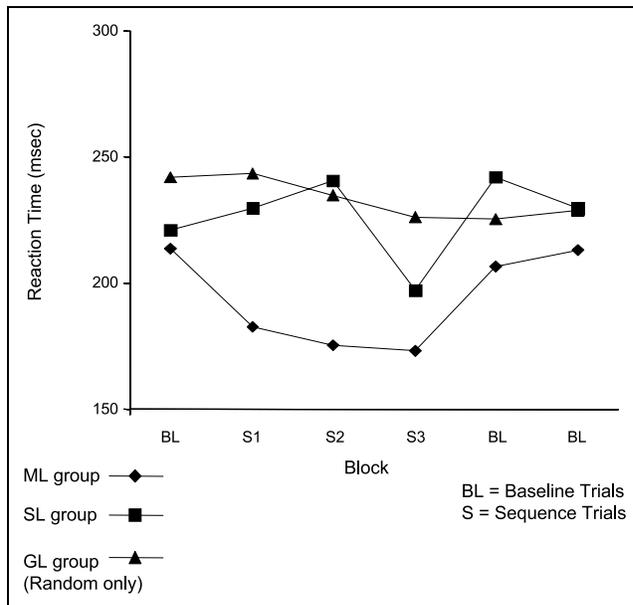


Figure 3. Facilitation of sequence learning. ML subjects have adapted to three visuomotor rotations and one gain change. They are faster at sequence learning than SL subjects. Each data point is the average RT across the block.

contrasts comparing performance on the last sequence block to that on the subsequent random block supported sequence learning for both the ML and SL groups [ML subjects, $F(1,19) = 19.0$, $p < .01$, $\omega^2 = .54$, large effect size; SL subjects, $F(1,19) = 4.1$, $p < .10$, $\omega^2 = .17$, large effect size; GL (random) subjects, $F(1,19) < 1.0$, $p > .50$]. Approximately one-third of both the ML and the SL subjects noticed the repeating pattern of target presentations and could report the target locations.

Multiple Learning Experiences Increase Susceptibility to Movement Perturbations

Following completion of the learning experiences, ML, GL, and SL subjects performed joystick-aiming trials for an additional three blocks. On occasional, random trials, the feedback was rotated by an amount that subjects had not previously experienced. The relative effect of the perturbation trials is plotted in Figure 4A for one ML and one GL subject. Qualitatively, the ML subject shows a greater relative effect of the perturbation, which extends into some of the nonperturbed trials. The cross-correlation function between perturbations delivered and errors made across trials is plotted in Figure 4B for one example ML and GL subject. The peak of the cross-correlation function was greater for the ML subjects than for the GL and SL subjects combined across the three blocks containing perturbation trials [Group \times Trial interaction, $F(1,83) = 3.9$, $p < .02$, $\omega^2 = .08$, medium effect size]. This difference

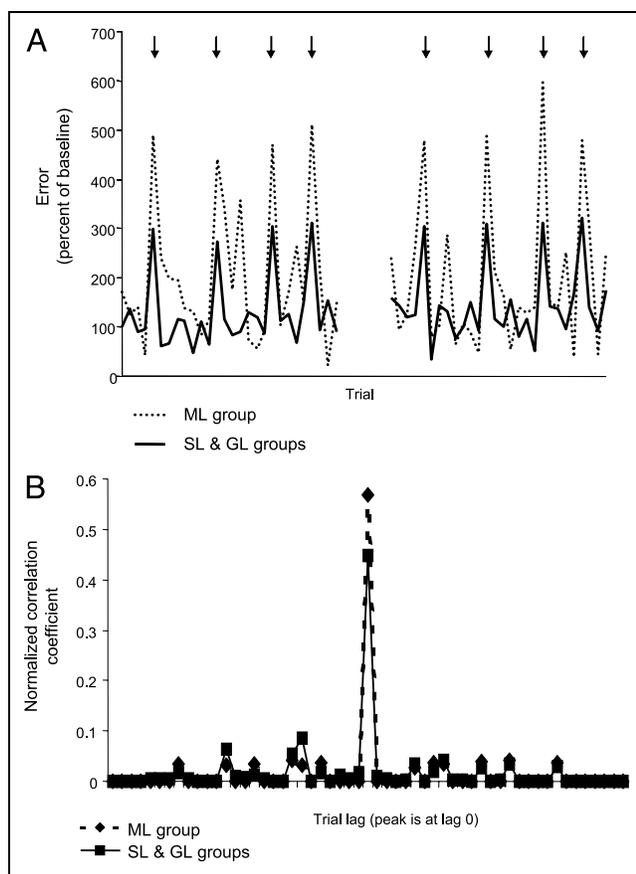


Figure 4. The impact of unpredictable perturbations on performance. (A) Relative effect of perturbation trials (indicated by the arrows) on endpoint errors for a representative ML and GL subject, for individual trials. (B) Coupling between perturbation delivery and performance across trials for another representative ML and GL subject. Coupling is higher for the ML subject.

was significant only at a zero trial lag, indicating that the perturbation effect on subsequent trials that is suggested by Figure 4A was not consistent across subjects.

Subjects Show Individual Differences in Their Learning to Learn Capacity

We employed a backward-stepping multiple regression procedure for each of the learning experiences to determine whether individual differences in the prior learning experiences predicted subsequent adaptation rates. This analysis was performed with ML subjects only. The analysis begins with all of the factors included (e.g., in the case of gain adaptation, the performance for each of the three rotations would be included in the initial model) to compute a multiple regression. Individual variables that do not contribute predictive value are removed from the model one at a time until the best multiple (or single) regression model remains. Individual differences in early adaptation performance (mean of the first three trials) at the third rotation were predicted by an individual's performance during early

adaptation of the first two rotations [$R = .57$, $F(2,16) = 3.8$, $p < .05$, $\omega^2 = .07$, medium effect size]. Additionally, differences in early gain adaptation across subjects were predicted by early rotation adaptation [multiple regression including R1, R2, and R3 performance, $F(3,15) = 2.8$, $p < .10$, $R = .60$, $\omega^2 = .03$, small effect size]. In both cases, the multiple regression model was the best fit. Early adaptation performance on the visuomotor tasks was not predictive of early sequence learning across subjects [$F(4,14) < 1.0$, $p > .50$, $R = .34$, $\omega^2 < .01$].

DISCUSSION

The transfer of adaptation across the three visuomotor rotations that we observed in this study is consistent with previous reports (Abeele & Bock, 2001a; Cunningham & Welch, 1994). Subjects are able to generalize from their prior learning experiences, such that new learning occurs more quickly. This is not surprising in the case of the three rotations, since they are all variants of the same task and the three rotations were similar in magnitude. The ML subjects that had first learned the three rotations adapted to the altered gain of display more rapidly than the GL subjects. This was not simply due to a greater facilitation with the joystick device and stimulus display, since the GL subjects had the same quantity of exposure to the experimental setup. The transfer effect was not large, likely due to the very rapid adaptation to the gain change by both experimental and control subjects. This transfer between the different visuomotor tasks replicates previous learning to learn findings (Bock et al., 2001; Roller et al., 2001). Although rotation adaptation, gain adaptation, and prism shift adaptation are thought to be somewhat strategically independent, they are all visuomotor adaptation tasks, requiring an updating of the mapping between visual and motor movement representations. Such visuomotor mapping relies on posterior parietal cortex and cerebellar regions (Ghilardi et al., 2000; Imamizu et al., 2000; Inoue et al., 1997, 2000; Clower et al., 1996). Learning to learn in this case may then reflect heightened plasticity in these regions due to their engagement in recent, prior learning experiences. That is, they may become primed for learning across the visuomotor adaptation tasks.

If heightened plasticity of the neural substrates mediating task behavior was the major mechanism mediating the learning to learn phenomenon, then the effect should have little or no transfer to motor sequence learning. Although sequence learning and visuomotor adaptation have some overlapping neural substrates, for the most part it is thought that sequence learning is both strategically and neurally different from visuomotor adaptation. That is, sequence learning relies more heavily on basal ganglia and medial motor area circuitry, while adaptation relies more heavily on cerebellar and parietal regions (cf. Seidler et al., 2002; Ghilardi et al., 2000; Imamizu et al., 2000; Hikosaka et al., 1999; Inoue

et al., 1997, 2000; Jueptner, Frith, Brooks, Frackowiak, & Passingham, 1997; Jueptner, Stephan, et al., 1997; Clower et al., 1996). The learning theory recently presented by Ungerleider, Doyon, and Karni (2002) and Doyon, Penhune, and Ungerleider (2003) proposes that the striatal and cerebellar systems both support the two types of learning, but following differing time courses. This theory suggests that, for early learning processes, both sequence learning and sensorimotor adaptation rely on the striatum and the cerebellum. Longer duration learning processes, retention, and consolidation differ between the two categories of learning, however, with the striatum preferentially involved in sequence learning and the cerebellum with adaptation (Doyon et al., 2003; Ungerleider et al., 2002). The faster rate of sequence learning that we observed for subjects that had participated in multiple visuomotor adaptation paradigms was quite unexpected. Since the group differences are largest during the early stages of learning, it is likely that these skills are specific to early learning processes. Thus, it may be that the overlapping neural substrates supporting the early stages of both sequence learning and sensorimotor adaptation as proposed by Doyon et al. (2003) and Ungerleider et al. (2002) allows for this between task transfer of learning.

Another potential mechanism contributing to this transfer is that subjects may have acquired some very general skills that can be applied to various types of motor learning. It is possible, for example, that learning-facilitated subjects are better at pattern detection, conflict monitoring, and error detection. These are all functions that have been attributed to the anterior cingulate cortex (cf. Liddle, Kiehl, & Smith, 2001; Botvinick, Nystrom, Fissel, Carter, & Cohen, 1999; Carter et al., 1998; Berns, Cohen, & Mintun, 1997), although the assignment of these functions is not without controversy (see Paus, 2001, for a review). It should be noted that the anterior cingulate is thought to play this novelty detection role even in the absence of conscious awareness of task changes (Berns et al., 1997). This is a region that is active during the early stages of skill learning (Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994), which is sensitive to changes in learning conditions (Berns et al., 1997; Jenkins et al., 1994) and which has been shown in the monkey to contain corticospinal projections, located near the vertical plane passing through the anterior commissure (Dum & Strick, 1991). Before learning processes can be engaged, the learner must first detect the existence of some predictable, and therefore learnable, pattern or effect, whether this occurs consciously or subconsciously. Thus, it may be that the anterior cingulate is becoming more engaged across these multiple learning experiences, allowing the skill acquisition process to become activated more quickly.

We observed a greater degree of coupling between the perturbations and performance in the learning-facilitated subjects than in the control subjects. Such

high coupling between environmental or task changes and movement performance is beneficial to learning, as long as task changes are consistent or predictable. When effects are transient or unpredictable, however, such coupling would be disadvantageous because it would be detrimental to maintenance of stereotypical behavior across trials. Zanone and Kelso (1992) have also reported a reduction in the stability of preexisting motor patterns associated with new learning. It is likely that this coupling reflects the cost of the learning to learn phenomenon, and may explain why we are not always capable of our maximum learning rates. We chose a perturbation stimulus that was similar to the learning stimuli (a rotation of a new magnitude). We expected that ML subjects would show evidence of trying to learn this stimulus (or attempts to generalize from their prior experiences), even when it was not occurring on a predictable basis. This hypothesis was not supported, however. The ML subjects did not show higher coupling between the perturbations and performance at trial lags greater than zero (cf. Thoroughman & Shadmehr, 2000). Additionally, although these subjects were able to effectively generalize from their prior learning experiences to new learning conditions, they demonstrated poorer performance on the perturbation trials than the single learning exposure subjects.

Since the coupling between the perturbations and performance was highest at a zero trial lag, the ML subjects must be operating with a different strategy or central set than the GL and SL subjects. One example of changing central set during the course of learning comes from Burdet, Osu, Franklin, Milner, and Kawato (2001). These authors demonstrated that limb stiffness can be modified in a task-dependent manner during learning (Burdet et al., 2001). Decreasing limb stiffness could be a useful method for the system to gain more information about environmental and task changes, when subjects are frequently exposed to new learning.

The single trial perturbation responses could also be reflective of strategic differences among the ML, SL, and GL groups. Recent work on transfer of visuomotor adaptation suggests that adaptive processes may proceed in two stages (Wang & Sainburg, 2003). These authors propose that the first trial of a new condition may serve to probe the environmental context, followed by a secondary stage in which subjects may call upon prior adaptive experiences. It is unclear how subjects would know to utilize the single trial strategy in our experiment, since our perturbations were delivered at unpredictable times. It may be, however, that multiple learning exposure subjects rely on this strategy to a differing extent than naïve learners. This could also potentially explain why the ML subjects appear to have a reduced response to the altered gain of display on the first trial in comparison to the GL subjects.

We have provided evidence that transfer of motor learning can occur not only between tasks with high

similarity, but also between very different tasks, when subjects are engaged in multiple learning experiences. Although we have proposed several potential mechanisms that might mediate this learning to learn phenomenon, it is highly likely that the mechanism of transfer differs depending on whether transfer is between skills that are variants of the same task or between skills that are neurally and strategically independent. This is supported by the correlation data showing that, although early learning rates are correlated across subjects for the visuomotor adaptation tasks, individual differences in sequence learning are not predicted by these visuomotor adaptation rates. Regardless of the underlying mechanisms, the results challenge the idea of specificity of learning and provide further support that multiple learning experiences can have a nonspecific, beneficial impact on sensorimotor adaptive processes. These findings increase our understanding of transfer of learning between conditions and have important implications for rehabilitation training. The data suggest that, for maximum transfer outside of the clinic, therapeutic training should encompass a variety of multiple motor learning experiences.

METHODS

Subjects

Thirty-three subjects participated in this study, ranging in age from 18 to 30 years old (mean age 21.9 years, standard deviation 3.6 years). Sixteen of the subjects were women and 17 were men. Four of the subjects were left-handed. All subjects signed an institution-approved human subjects consent form prior to their participation. Subjects were compensated with experimental course credit for their participation, which took an average of 3 hr over two testing days.

Procedure

Subjects performed several variants of a basic joystick-aiming task. All movements had the same start position in the center of the computer display screen. We used a dual potentiometer joystick device to track hand movements in two dimensions. The joystick was secured to the table in front of the subjects, placed at their body midline. For each trial block, targets could appear in one of four directions: up, right, down, or left of the central start position. Targets were 4.8 cm from the start position (center to center distance) and were 0.8 cm in diameter. Subjects were instructed to move the cursor representing the joystick position into the target as quickly as possible upon target appearance and to hold the cursor within the target until it disappeared (3 sec following its appearance). Subjects were instructed to release their grip on the joystick handle at this point, allowing the spring-loaded device to recenter for the next trial. The

subsequent trial began 2 sec later, resulting in an intertrial interval (from one target presentation to the next) of 5 sec.

ML subjects ($n = 19$) learned five different tasks under this basic paradigm over two test sessions (conducted on separate days, within approximately 48 hr of each other). On the first day, they adapted to three different visuomotor rotations: 15°, 30°, and 45° counterclockwise rotations of the cursor position about the central start location (cf. Cunningham & Welch, 1994). They then readapted to the traditional cursor mapping in between each adaptive exposure. The trials were presented as follows:

B1 baseline (BL, no rotation), 24 trials
 B2 baseline (BL, no rotation), 24 trials
 B3 rotation 1 (A1), 28 trials
 B4 rotation 1 (A2), 28 trials
 B5 rotation 1 (A3), 28 trials
 B6 baseline (BL, no rotation), 28 trials
 B7 baseline (BL, no rotation), 28 trials
 B8 rotation 2 (A1), 28 trials
 B9 rotation 2 (A2), 28 trials
 B10 rotation 2 (A3), 28 trials
 B11 baseline (BL, no rotation), 28 trials
 B12 baseline (BL, no rotation), 28 trials
 B13 rotation 3 (A1), 28 trials
 B14 rotation 3 (A2), 28 trials
 B15 rotation 3 (A3), 28 trials
 B16 baseline (BL, no rotation), 28 trials
 B17 baseline (BL, no rotation), 28 trials

Ten of the subjects (ML1) acquired the visuomotor rotations in the following order: 30°, 15°, 45° while nine (ML2) acquired them in the order: 45°, 15°, 30°. This counterbalanced design allowed us to assess generalization of learning for subjects that learned the 45° rotation last in comparison to those that learned it first, and for subjects that learned the 30° rotation last in comparison to those that acquired it first.

On the second day, the ML subjects first adapted to a change in the gain of display of their movements, then they learned a repeating sequence of four target locations, and finally they performed several blocks of baseline trials with occasional perturbation trials. The trials were presented as follows:

B18 baseline (BL, no learning stimulus), 24 trials
 B19 baseline (BL, no learning stimulus), 24 trials
 B20 altered gain (G1), 28 trials
 B21 altered gain (G2), 28 trials
 B22 altered gain (G3), 28 trials
 B23 baseline (BL, no learning stimulus), 28 trials
 B24 baseline (BL, no learning stimulus), 28 trials
 B25 sequence (S1), 28 trials
 B26 sequence (S2), 28 trials
 B27 sequence (S3), 28 trials
 B28 baseline (BL), 28 trials

B29 baseline (BLP), 28 trials (with 4 perturbation trials interspersed)

B30 baseline (BLP), 28 trials (with 4 perturbation trials interspersed)

B31 baseline (BLP), 28 trials (with 4 perturbation trials interspersed)

We increased the gain of display of movements by a factor of 1.5 for the altered gain blocks. The sequence blocks consisted of the following repeating target sequence: up, left, right, down. This is not just a simple four-element sequence however. Subjects were required to return to the central start position between each target (passively), increasing the effective sequence length to eight elements. There were four perturbation trials in each of blocks 29, 30, and 31. This perturbation consisted of a cursor position rotation of 25° in a counterclockwise direction.

Thirteen control subjects also participated in these experiments. These subjects performed the same number of trials on Day 1 as the experimental subjects, but did not receive any trials in which the cursor position was rotated. That is, all trials performed were baseline trials. Seven of these subjects adapted to the altered gain of display on Day 2 (GL) and six learned the sequence (SL). These subjects performed the baseline-aiming task in all other blocks on Day 2. These subjects also received the perturbation trials during the last three target blocks.

Subjects were not informed in advance as to whether the upcoming block contained a learning stimulus (rotation, gain change, or sequence). They were instructed to hit the target as rapidly as possible, and to attempt to minimize both RT and movement time. Following the first sequence block, subjects were probed about their awareness of the existence of the sequence. We asked them the following questions: “Did you notice anything different about the last block? If so, what?” Following the final sequence block, we asked subjects: “Did you notice the sequential target presentation over the last three blocks?” They were asked to attempt to report the target sequence regardless of whether they had noticed its existence.

Data Analysis

We analyzed the joystick data offline, using custom data analysis routines. We first filtered the data with a dual-pass Butterworth digital filter (cf. Winter, 1990) using a cutoff frequency of 10 Hz. Then we computed the resultant joystick path by taking the square root of the sum of the squared x and y coordinate data at each time point. The tangential velocity profile was then computed via differentiation. Movement onset and offset were calculated by applying the optimal algorithm of Teasdale, Bard, Fleury, Young, and Proteau (1993) to this velocity profile for each movement. We computed the RT by subtracting the time of the stimulus presentation from

the time of the onset of movement. This variable was used to assess sequence learning.

Subjects typically make multiple submovements to achieve targets early in the sensorimotor adaptation process (cf. Seidler, Bloomberg, & Stelmach, 2001a, 2001b; Cunningham & Welch, 1994). Since our focus of interest was more in how the subjects preplanned the movements (reflective of learning) and less in the on-line corrections that they made, we decomposed the movement into its primary and secondary submovements (Meyer, Abrams, Kornblum, Wright, & Smith, 1988). We then determined the distance from the target at the end of the initial ballistic impulse, labeled as IEE. The algorithm we used searches for a period of acceleration following a period of deceleration or a change in the sign of velocity. Thus, the initial preplanned movement has “ended” when there is either a change in movement direction or an additional propulsive action is made. This method results in a measure that is little if at all influenced by feedback processes (cf. Seidler-Dobrin & Stelmach, 1998; Elliott, Carson, Goodman, & Chua, 1991). IEE was computed as the distance from the center of the targets; therefore, all IEE numbers less than 4 mm were within the target circle. We evaluated the IEE as an indicator of learning the rotated feedback and the altered gain of display. We determined the effect of the perturbation trials on performance by examining the coupling between the perturbation trial schedule and IEE across individual trials. This was done by computing the cross-correlation function between the perturbation schedule and the subjects’ error performance across trials for each of the three perturbation blocks. The peak of this function (PCC, at a lag of zero trials) was used to compare susceptibility to the perturbation trials between the control and experimental subjects.

We used repeated measures analyses of variance (RM ANOVA) designs on the variables (RT, IEE, and PCC) to examine rate of learning. These analyses were conducted using the following form: Group (2) \times Block (17 for Experiment 1, 7 for Experiment 2, and 3 for Experiment 3) \times Trial (28 or 24 per block). Significant interactions were followed up with simple contrasts. The Huynh–Feldt epsilon (Huynh & Feldt, 1970) was evaluated to determine whether the repeated measures data met the assumption of sphericity ($\Sigma > 0.75$). In cases where sphericity was met, the univariate tests were used to maintain power. Otherwise, the repeated measures were treated as multivariate. Note that the significance of the F value is assessed using different degrees of freedom, depending on whether the univariate or multivariate tests are used. ω^2 , an estimate of the total population variance that is explained by the variation due to the treatment (Keppel, 1991), was computed for all effects. Its value does not depend on sample size or power of the experiment. Its values can range between 0.0 and 1.0, with negative values a possibility when the

associated F value is less than 1.0. Cohen suggests that a small effect is comparable to a ω^2 of 0.01, a medium effect is 0.06, and a large effect is 0.15 or greater (Cohen, 1977). These standards were employed in our assessment of treatment effect sizes.

We computed multiple regression analyses to determine whether subjects show individual differences in the capacity for facilitated learning and to examine the evolution of learning facilitation across the different tasks. We used the average error of the first three data points from each of the rotations and the gain change and the average RT from the first three sequence repetitions in these analyses. Only experimental subject data were included in these analyses. Backward-stepping multiple regressions were used to determine whether individual differences in the first two rotation exposures predict individual differences at the third rotation, whether rotation individual differences predict gain adaptation differences, and whether the four visuomotor adaptation experiences are predictive of early sequence learning performance across individual subjects.

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