Protection of savings by reducing the salience of opposing errors

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Abstract

When humans encounter the same disturbance twice, they adapt to it faster during the second exposure. To examine how subconscious learning systems contribute to this savings process, previous studies have suppressed explicit awareness of the perturbation by gradually increasing its magnitude during initial learning. This has produced mixed effects, with some studies demonstrating faster relearning, and others observing no acceleration during relearning. Here we examined whether these differences might be due to the nature of a de-adaptation period that separates two learning periods. To test this idea, we manipulated the magnitude of washout errors by de-adapting participants abruptly, gradually, or by removing feedback entirely. Empirical analyses indicated that the different classes of washout errors had a profound effect on savings: large washout errors nullified the ability to save, whereas small errors or the absence of error protected savings. Model-based analyses suggested that changes in learning rates were mediated by an increase in sensitivity to error that could be reversed by experience with oppositely-oriented washout errors. This suggests that the experience of error produces both a facilitation of learning for similar errors and a reduction in learning for dissimilar errors. The latter can abolish the expression of savings following gradual adaptation.

Introduction

When an unexpected perturbation to our motor system occurs, the resulting errors in our actions and predictions[1–5] update our motor commands, predictively countering future disturbances. The removal of a perturbation causes behavior to rapidly revert to its initial state, but a lingering memory of our initial encounter is stored within the nervous system, whereby re-exposure to the perturbation results in more rapid adaptation. This learning hallmark, termed savings[6], can occur on the same day, overnight[7], or even a year after the initial disturbance[8], and is ubiquitous across effectors including saccade adaptation[9], locomotion[10,11], visuomotor adaptation[7,12,13], force field adaptation[14–16], and conditioning paradigms[17]. What components of adaptation experiments are necessary to produce savings during re-learning phases?

Our ability to flexibly increase our learning rate is known to rely on two parallel adaptive systems: an explicit process directed by our conscious strategies[18–20], and a subconscious implicit process that operates without our awareness[2,4]. The implicit and explicit contributions to savings have been typically studied using visuomotor rotations, a paradigm that can provide an opportunity to parse adapted responses into a re-aiming direction (*i.e.*, the explicit strategy) and an additional uncontrolled adjustment (*i.e.*, the implicit correction)[18].

In visuomotor adaptation, improvements in strategy use are salient in protocols where a rotation is abruptly initiated during two separate exposures. Explicit savings can be documented by quantifying strategy use via reaction time manipulations[7,21], or by directly querying subjects[12]. When conditions are applied to suppress explicit strategies, such as limiting response time[22], or minimizing errors experienced during initial learning[23], implicit savings can be isolated. This latter minimization approach is performed by gradually introducing a perturbation, thus maintaining a

small discrepancy between the disturbance and motor action that produces smaller error sizes that go undetected, limiting strategy use[23].

Intriguingly, however, studies that have employed gradual perturbations have observed mixed effects on the ability of *gradual* learning to facilitate more rapid *abrupt* learning. Absence of savings following gradual learning[24] is consistent with a memory of errors model[24,25], in which gradual adaptation cannot improve abrupt adaptation due to a mismatch in error size: errors are large in the abrupt case, but small in the gradual case. Thus, to the brain, an abrupt perturbation following gradual adaptation may appear to be a novel context, because large errors it experiences never occurred in the past. While this prediction is consistent with at least one prior study[24], more recent work has exhibited opposing results where gradual adaptations improve abrupt learning rates[23,26], particularly through an acceleration in implicit learning[23]. How is it that gradual perturbations result in savings in some experiments, but not in others?

Here we consider the possibility that typical sensorimotor learning paradigms may fail to produce savings not because of differences in the way individuals learn, but rather by the way they forget. That is, savings protocols require not only two learning periods, but also the decay of the adapted behavior in between the two learning phases. This forgetting is achieved in a washout period in which the perturbation is removed to return the adapted state to its baseline level. The conditions used to achieve this washout, however, vary across studies. In some cases, washout consists of abrupt cessation of the perturbation, and lasts the same number of trials as the initial exposure period[24]. On the other hand, some savings experiments employ much shorter washout phases[23,26] that are preceded by other conditions such as invariant error-clamp[26] or no-feedback[23] trials.

Critically, these differences in the washout period alter the size of errors experienced by the subject. Could it be that *larger* washout errors experienced over *longer* durations reduce the ability to save? This idea seems plausible, given that washout produces errors that are opposite in sign to the errors experienced during adaptation phases, thus necessitating a learning response in the opposite direction. Here we examine the overlooked possibility that the nature of washout plays a central role in the expression of savings. Across three groups, we manipulate the types of washout errors by (1) removing errors entirely by eliminating visual feedback, (2) limiting the size of errors by de-adapting subjects gradually, or (3) facilitating large errors by abruptly disengaging a visuomotor rotation. We then apply empirical and model-based approaches to assess whether some washout conditions more easily produce savings during abrupt rotation periods that follow initial gradual learning phases. These experiments seek to not only clarify previous discrepancies in the literature, but also to expand our current models of savings in the implicit learning system.

Materials & Methods

Participants

40 healthy volunteers (18-35 years old; 18 females) participated in this study. All subjects were right-handed as assessed by the Edinburgh handedness inventory (Oldfield, 1971). Informed consent was given by each participant, and consent forms were approved by the University of Wisconsin-Milwaukee Institutional Review Board. Subjects were randomly assigned to 1 of 4 groups: 3 gradual rotation groups and 1 control group.

Apparatus

Participants were situated in a robotic exoskeleton (KIMARM, BKIN Technologies Ltd, Kingston, ON, Canada) that provided gravitational support to the right arm (all subjects used this arm in the present study). The exoskeleton was positioned so that the arm was hidden underneath a horizontal display (Fig. 1A). To track the hand's position, a small cursor was projected onto the display, over the subject's index fingertip. During each trial, the KINARM projected visual stimuli onto the display, so that they appeared in the same plane as the arm. The visual stimuli consisted of a centrally located start circle (2 cm in diameter) and 1 of 4 target circles (2 cm in diameter) located 10 cm away from the start target (Fig. 1A). We sampled the hand's position in the x-y plane at 1000 Hz. Position data were low-pass filtered at 15 Hz, and then differentiated to calculate velocity. Post-processing, analysis, and modeling were conducted in MATLAB R2018a (The MathWorks Inc., Natick, MA).

Experimental Design

Participants were assigned to 1 of 3 experimental groups (n=10/group). Each experimental group experienced 4 experiment phases: (1) a baseline reaching period, (2) a gradual adaptation period, (3) a washout period, and (4) an abrupt readaptation period (Fig. 1B). During the gradual learning period, a rotation was introduced that slowly increased in magnitude (up to 24°). In the abrupt readaptation period, the rotation immediately attained its maximum value. To determine how gradual learning and washout type altered reaching behavior during the final abrupt learning phase, we compared behavior to a control group (n=10) that completed the same 4-phase

122 adaptation paradigm, with the only exception being that the perturbation was introduced
123 abruptly, not gradually, in the initial adaptation period.

124 In the baseline period (Fig. 1B, baseline), participants moved their arm to each of the four
125 targets over a 10-cycle reaching period. On each trial, continuous visual feedback was provided
126 via a cursor indicating the location of the index fingertip. Participants were instructed to move
127 rapidly and accurately to the target location. The trial ended 1.5 sec after target presentation. To
128 begin the next trial, the participants brought their hand back to the central start position.
129 Throughout the entire experiment, the four targets were presented in a pseudorandom order in
130 4-trial cycles (i.e., all four targets presented once in a cycle).

131 During the gradual adaptation period, participants were exposed to a visuomotor rotation
132 that systematically increased in size throughout the session. It started at 0° for 9 cycles, increased
133 by 1° (i.e., visual display of the cursor rotated 1° counterclockwise (CCW) about the start circle)
134 for next 23 cycles, and remained at 24° for last 8 cycles (Fig. 2A, gradual rotation). We provided
135 visual feedback on all trials. Following this session, participants underwent a washout period. This
136 washout period was the critical manipulation in our study and differed across all 3 gradual
137 learning groups. One group experienced a no-feedback condition in which the cursor was
138 removed during movement execution. Another group experienced abrupt washout in which
139 visual feedback was given and the rotation was immediately set to 0° (*i.e.*, the baseline
140 condition). Last, a third group experienced gradual de-adaptation: the rotation schedule was
141 identical to the initial gradual adaptation sequence, but in the reverse order (9 cycles 24°, 23
142 cycles in which the rotation decreased by 1°, 8 cycles with 0° rotation). Note that the control

group, that initially experienced an abrupt rotation condition, de-adapted in the no-feedback condition in between rotation exposures.

The experiment ended with an abrupt readaptation period that lasted 40 cycles (160 trials total). During this session, the cursor was immediately rotated 24° CCW relative to the hand path (Fig. 1A, readaptation period). This last abrupt adaptation was used to examine whether gradual or abrupt learning, followed by varying washout conditions, would lead to savings during a second rotation period.

Empirical Data Analysis

Data analysis was conducted in MATLAB (MathWorks, Natick, MA). To quantify performance, we calculated the reaching movement angle at peak velocity. This angle was computed as the hand's angular position relative to a line segment connecting the start and target positions. We removed outlier reach angles, by first removing angles with an absolute value greater than 60° (0.567% of trials), and then removing angles that deviated by more than 5 median absolute deviations within all trials in a given cycle, collapsed across participants in a specific experimental group (1.798% of trials). Next, data were averaged within each 4-trial cycle.

To empirically compare adaptation between groups, we assessed the learning rate during each abrupt rotation phase via an exponential function. We focused on rate measures, to prevent our evaluation from being biased by the initial state of the learner (*i.e.*, subjects may demonstrate greater total adaptation not because they learn more rapidly, but because their initial reach angle is greater during the second abrupt rotation due to incomplete washout from the initial rotation). Thus, we fitted an exponential curve to participant hand angles, and used the rate parameter as

our measure of learning rate. For this, we employed a 2-parameter exponential function designed to enforce that each curve begins at the initial pre-rotation reach angle. For the initial perturbation in the control group, this hand angle was computed as the average angle over the last 4 baseline cycles. For the abrupt rotations during the second exposure period (across all groups), this angle was computed as the average angle over the last 4 washout cycles. The exponential function took the mathematical form:

$$y(t) = \alpha - (\alpha - y_0)e^{-\beta t} \quad (1)$$

Here, α is parameter that encodes the exponential curve's asymptote, y_0 is the initial reach angle described above, β is the rate parameter of interest, $y(t)$ is the reach angle on cycle t (starting at $t = 0$). The function was fit to 41 cycles of data at a time (40 cycles of the abrupt rotation plus the initial reach angle cycle on $t = 0$) using a bounded least-squares approach (MATLAB *fmincon*). The parameter search was repeated 100 times, each time varying the initial parameter estimate that seeds the algorithm. The α parameter was bounded between -45° and 45°. The β parameter was bounded between 0 cycle^{-1} and 0.5 cycle^{-1}. The model parameters that minimized squared error across all 100 repetitions were selected.

State-space learning model

To interpret our empirical results using an error-based learning framework, we employed a state-space model[15,22,25,28,29,31]. The model describes adaptation as a trial-by-trial learning process whereby the adapted state of the individual is updated by (1) learning from the error experienced on each trial and (2) a small amount of decay that reflects temporal instability of short-term

187 adaptation[30,48,49]. In the model, the total update in the motor memory due to an error is
188 controlled by one's sensitivity to error (*b*) and the strength of memory retention between trials
189 is encoded by a retention factor (*a*). Together, learning and forgetting collectively determine how
190 the subject's internal state (*x*) evolves in response to an error (*e*) experienced on trial *t* in the
191 presence of Gaussian state noise (ε_x, normally distributed with zero mean, and standard
192 deviation of σ_x) according to:

193 $$x^{(t+1)} = ax^{(t)} + be^{(t)} + \varepsilon_x^{(t)} \quad (2)$$

194 Eq. (2) allows us to ascribe performance differences during the adaptation period to interpretable
195 quantities: retention (*a*) and error sensitivity (*b*).

196 Note, however, that the internal state (*x*) is not a measurable. Instead, on each cycle, the
197 motor output (reach angle) is measured. The reach angle (*y*) directly reflects the subject's internal
198 state, but is altered by execution noise (ε_y, normal with zero mean, std. dev. = σ_y) according to:

199 $$y^{(t)} = x^{(t)} + \varepsilon_y^{(t)} \quad (3)$$

200 Together, Eqs. (2) and (3) represent a single module state-space model. We fit this model to each
201 participant's reach angles during the adaptation period using the Expectation-Maximization (EM)
202 algorithm[28]. For each adaptation period, all 40 abrupt rotation cycles and 3 preceding baseline or
203 washout cycles were included. EM is an algorithm that conducts maximum likelihood estimation
204 in an iterative process. We used EM to identify the parameters $\{a, b, x_1, \sigma_x, \sigma_y, \sigma_1\}$ that maximized
205 the likelihood of observing the data (x_1 and σ_1 represent the subject's initial state and variance,
206 respectively). We conducted 100 iterations, each time modifying the initial parameter guess that
207 seeded the algorithm. The retention factor (*a*) was bounded between 0.85 and 1. The initial state
208 (x_1) was bounded between -10 and 20°. Error sensitivity (*b*) was bounded between 0 and 1. Last,

209 all 3 variance parameters were bounded between $1.0e^{-3}$ and 100. We selected the parameter set
210 that maximized the likelihood function across all 100 iterations.
211
212 *Statistics*
213 For statistical comparisons between 2 groups or conditions, paired or independent two-sample
214 t-tests were employed. When more than 2 groups were compared, we applied one-way ANOVAs.
215 For post-hoc testing, we used Dunnett's test to measure differences between each experimental
216 group and the control group (we reached analogous conclusions when Tukey's test was used for
217 post-hoc comparisons across all groups without specifying a control condition).
218
219 **Results**
220 Participants executed point-to-point movements between a start location and a target (Fig. 1A).
221 In each group, a visual rotation was applied to the cursor motion in two separate exposure
222 periods: a condition which generally leads to an increase in learning rate called savings. Here, we
223 altered the size of errors experienced in the washout period between each exposure (Fig. 1B) to
224 examine which conditions protect or abolish visuomotor savings.
225
226 *Visuomotor adaptation during point-to-point movements is accelerated by visuomotor savings*
227 Adaptation to a novel visuomotor rotation is often studied in the context of "slicing" movements
228 in which participants rapidly move a cursor through a target location without online feedback
229 corrections. Here, we trained subjects to execute point-to-point reaches that require accurate
230 endpoint control. To confirm that our point-to-point design also produces visuomotor savings as

we recently reported[27], we tested participants in our control group. After a short baseline period, a 24° rotation was abruptly introduced. Over time subjects adapted their reach angles to partially counter the disturbance (Fig. 1C, abrupt rotation). To washout this initial learning, we removed visual feedback, causing reach angles to gradually decay towards their baseline state (Fig. 1C, no feedback). To determine whether the learning system was improved by prior experience, we abruptly introduced a second 24° abrupt rotation, causing a rapid change in reach angle (Fig. 1C, abrupt rotation). How did learning in this second exposure period compare to naïve adaptation?

To answer this question, we isolated the two learning periods and fit an exponential curve to each participant's reach angles during both adaptation phases (Fig. 1D). As expected, the prior exposure to the rotation accelerated adaptation, almost doubling the subjects' learning rates (Fig. 1E; paired t-test, $t(9)=6.8$, $p<0.001$, Cohen's $d=2.15$). In sum, we find that point-to-point adaptation to a 24° rotation produces savings and is amenable to further study.

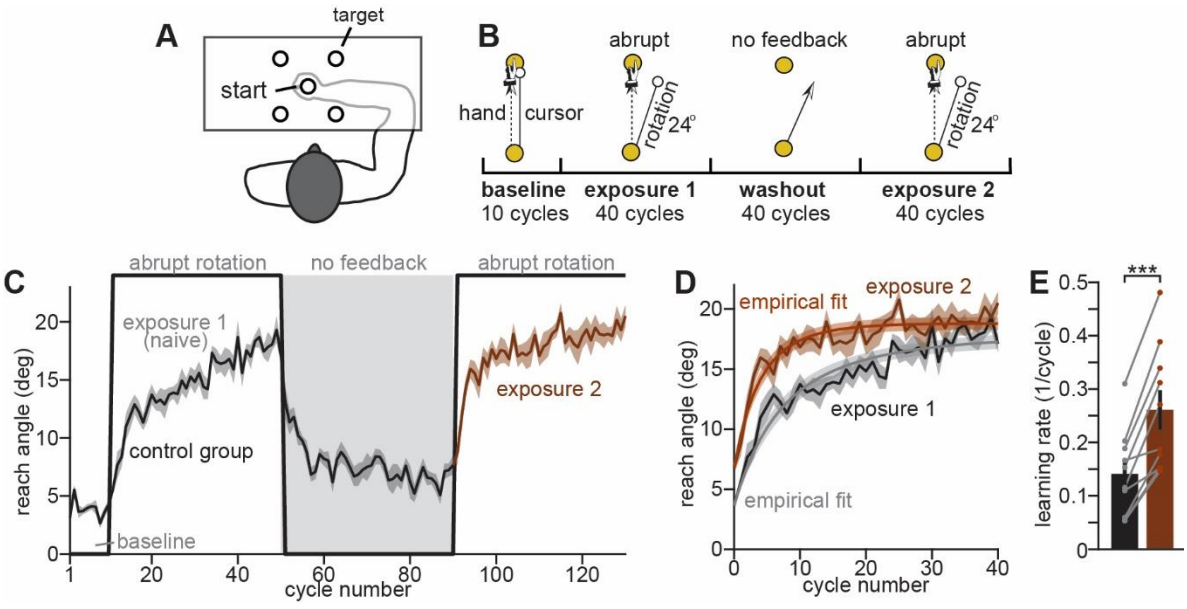

Figure 1. Savings in a point-to-point visuomotor rotation task. **A.** Experiment apparatus. Subjects were seated in a KINARM exoskeleton and executed point-to-point reaching movements to 1 of 4 targets. **B.** Perturbation schedule. The control experiment consisted of 4 experimental periods: (1) 10-cycle baseline

period, (2) abrupt 24°, 40-cycle rotation (exposure 1), (3) 40-cycle no visual feedback washout, (4) 40-cycle re-exposure to the 24° rotation (exposure 2). **C.** Learning curves. The reach angle at maximum velocity was calculated on each trial and averaged within each 4-trial cycle. **D.** Savings visualization. The learning curves during the first and second exposure to the rotation are shown. We fit a 2-parameter exponential curve to individual participants to quantify learning rates. The empirical model fit (empirical fit) is also shown overlaid on the measured learning curves (exposure 1 or exposure 2). **E.** Quantification of savings. We compared the learning rate parameters across the first and second exposures quantified via the exponential model fit in **D**. Errors bars indicated mean ± 1 standard error of the mean. Single points in **E** represent individual participants. Statistics: *** indicates $p<0.001$.

Abrupt and gradual perturbation exposures similarly enhance the rate of learning

Past studies have yielded conflicting evidence as to the necessary conditions for savings. In some cases, savings appears to require the experience of similarly sized errors during the initial and the re-exposure phases of the experiment[24]. This is achieved by creating large errors in each adaptation period via an abrupt perturbation. More recently, however, other studies have observed savings without the experience of large errors[23,26]. In this case, the rotation is introduced in a gradual manner whereby its magnitude slowly increases during the initial exposure. Do gradual rotations lead to savings in point-to-point reaching movements?

To answer this question, we tested a second group of participants in a gradual adaptation paradigm (Fig. 2A). Whereas the abrupt group in Fig. 1 experienced a 24° perturbation all at once, subjects in the gradual group experienced a time-varying rotation that grew 1° over 24 cycles to reach its terminal value. This dramatically slowed the rate of initial adaptation (Fig. 2B, compare blue: gradual and black: abrupt). After this initial exposure, participants in the gradual and abrupt groups experienced identical trial conditions: a no-feedback washout period in which the adapted hand angles returned to their baseline state (Fig. 2B, no feedback), followed by a second rotation that was introduced abruptly in both groups.

To determine how the initial exposure to the rotation modulated savings, we isolated the adapted reach angles during the second exposure period (Fig. 2C) and fit an exponential curve to each participant's performance across both groups. Intriguingly, we did not detect a statistically significant difference in learning rates (Fig. 2D; t(18)=0.328, p=0.747, Cohen's d=0.147), suggesting that abrupt and gradual exposures both lead to visuomotor savings.

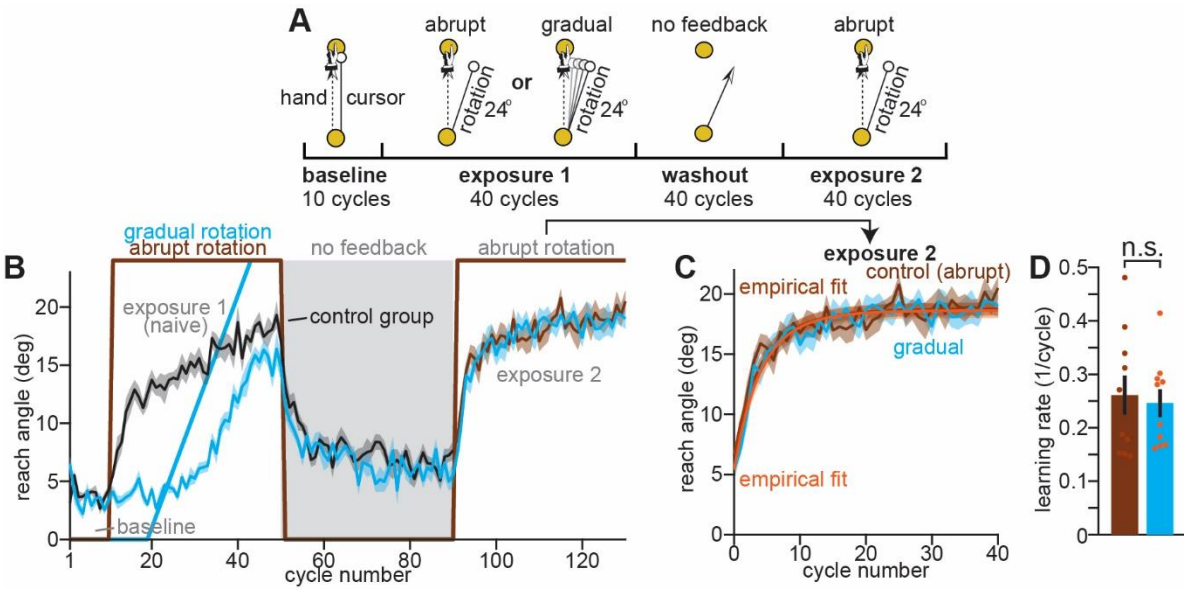

Figure 2. Abrupt and gradual adaptation lead to similar expression of savings in a point-to-point reaching task. **A.** Perturbation schedule. Two groups were tested in an experiment consisting of 4 phases: baseline, initial perturbation, washout, secondary perturbation. Groups differed only based on the visuomotor rotation encountered during the initial exposure: the control group from Fig. 1 experienced a 24° rotation that immediately reached its terminal value (labeled abrupt here), and the gradual group experienced a rotation that slowly increased in magnitude across 24 cycles to reach the same terminal value. **B.** Learning curves. The reach angle at maximum velocity was calculated on each trial and averaged within each 4-trial cycle. The control group (black during exposure 1, and brown during exposure 2) behavior is compared to the gradual group (cyan) behavior. The perturbation schedules are also shown overlaid with the data. **C.** Savings visualization. The learning curves during the second exposure period are shown; both groups adapted to an abrupt rotation during this period. We fit a 2-parameter exponential curve to individual participants to quantify learning rates. The empirical model fit (empirical fit) is shown overlaid on the measured learning curves (abrupt or gradual). **D.** Quantification of savings. We compared the learning

291 rate parameters during the second exposure period quantified via the exponential model fit in **C**. Errors
292 bars indicated mean ± 1 standard error of the mean. Single points in **D** represent individual participants.
293 Statistics: n.s. indicates $p > 0.05$.

294

295 *Size of error during washout modulates the strength of visuomotor savings*

296 Our results in Fig. 2 add to a growing body of evidence that savings can be achieved via a gradual
297 exposure to a perturbation, suggesting that large errors are not explicitly required to facilitate an
298 increase in learning rate. Why have some prior studies not observed the same result? Is it possible
299 that disagreement across studies is caused not by perturbation conditions, but rather by the type
300 of error experienced during the intervening period of washout that separates two adaptation
301 phases?

302 In Figs. 1 and 2, abrupt and gradual group subjects were de-adapted in a no-feedback
303 condition, preventing the experience of all visual errors. The absence of error led to a gradual
304 decay in reach angles, reproduced in Fig. 3B (cyan). To assess whether this de-adaptation
305 condition can alter the expression of savings, we tested two additional gradual groups (Fig. 3A)
306 that differed only by the errors experienced during washout. In the abrupt washout group, the
307 perturbation immediately ceased at the end of the initial adaptation period, creating large
308 oppositely-signed errors that induced rapid unlearning in the subsequent washout phase (Fig. 3B,
309 green). In the gradual washout group, the rotation was slowly decreased from cycle-to-cycle
310 during the washout period. This prevented the occurrence of large oppositely-signed errors,
311 leading to gradual unlearning of the initial adapted reach direction (Fig. 3B, magenta).

312 Next, all 3 gradual learning groups were exposed to an abrupt 24° rotation. To determine
313 how preceding washout modulated subsequent learning rates, we compared reach angles during

this abrupt readaptation period to those measured in naïve participants that had not previously experienced a rotation (*i.e.*, the initial adaptation period in the control group examined in Fig. 1). As before, we fit exponential curves to participant reach angles to empirically quantify individual subject learning rates (Fig. 3C). Intriguingly, we observed that washout conditions had a dramatic effect on re-learning rates (Fig. 3D, one-way ANOVA, $F(3,36)=4.97$, $p=0.006$). Namely, savings was observed only after no-feedback (post-hoc Dunnett's test, $p=0.019$) and gradual washout (post-hoc Dunnett's test, $p=0.019$), but not after abrupt washout (post-hoc Dunnett test, $p=0.987$).

In sum, the ability to express savings after gradual learning is modulated by the errors the participant experiences during de-adaptation. When large errors occur, as in our abrupt washout group, savings is eliminated. When errors are small (*i.e.*, gradual washout) or are removed during washout (*i.e.*, no feedback), savings is preserved.

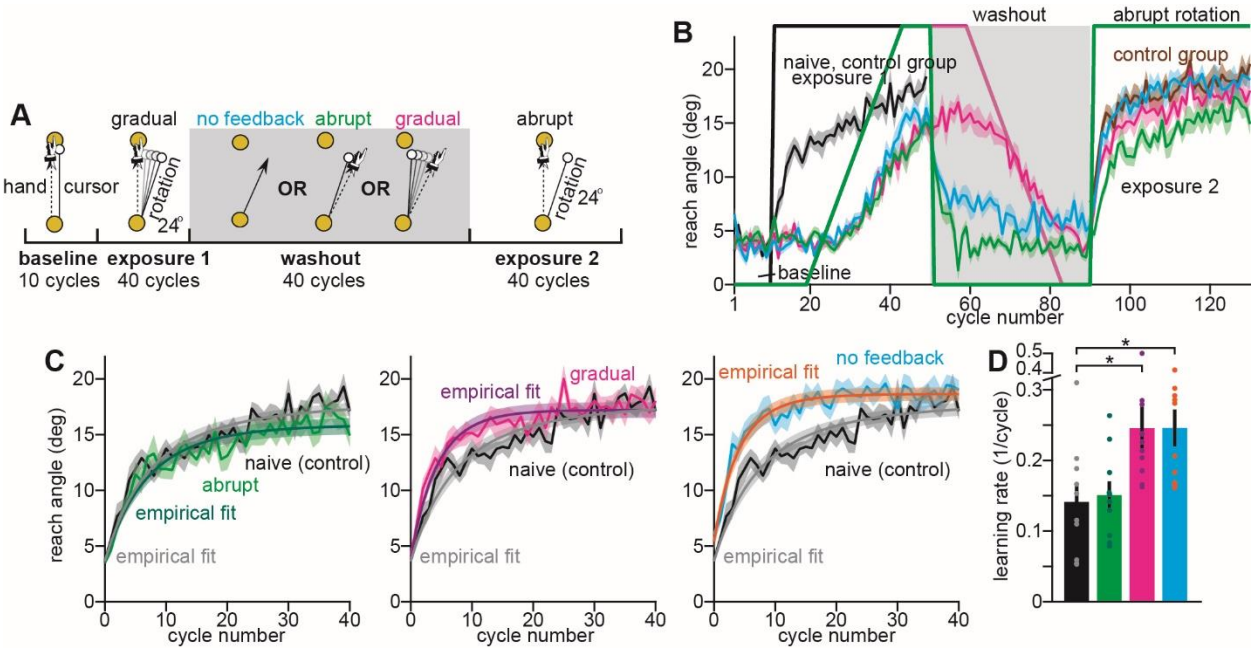

Figure 3. Savings after gradual learning is attenuated by washout error magnitude. **A.** Perturbation schedule. Three groups were tested in an experiment consisting of 4 phases: baseline, initial perturbation, washout, secondary perturbation. All groups experienced a gradual perturbation during the initial learning

period, and an abrupt rotation during the second exposure. Groups differed only based on the errors experienced during the washout (de-adaptation) phase. One group de-adapted in the absence of visual feedback (cyan, no feedback). A second group de-adapted in the presence of large errors due to the abrupt removal of the rotation (abrupt, green). A third group de-adapted in the presence of small errors due to the gradual removal of the rotation (gradual, magenta). **B.** Learning curves. The reach angle at maximum velocity was calculated on each trial and averaged within each 4-trial cycle. The abrupt group (black and brown) behavior is compared to all 3 gradual group from described in inset **A**. The perturbation schedules are overlaid with the data. **C.** Savings visualization. The learning curves during the second abrupt exposure period are shown. Each gradual group is shown in a separate inset (left: abrupt de-adaptation, middle: gradual de-adaptation, right: no-feedback de-adaptation). All learning curves are overlaid with the naïve performance of the control group that experienced the initial rotation abruptly. We fit a 2-parameter exponential curve to individual participants to quantify learning rates. The empirical model fit (empirical fit) is shown overlaid on the measured learning curves (naïve, abrupt, gradual, or no feedback). **D.** Quantification of savings. We compared the learning rate parameters during the second exposure period in each gradual group to the learning rate parameters in the initial abrupt exposure of the control group. Errors bars indicated mean ± 1 standard error of the mean. Single points in **D** represent individual participants. Statistics: * indicates $p < 0.05$.

Savings following gradual learning is promoted by an increase in sensitivity to error

Short-term sensorimotor adaptation is due to the combined effects of two processes: (1) trial-to-trial error-based learning, and (2) trial-to-trial forgetting[15,22,25,28–31]. In principle, savings could be caused by either an increase in the amount of learning that follows the experience of an error, an increase in the amount of learning retained with the passage of time, or a combination of both sources. These two processes can be captured by a state-space model that represents adaptation as a recursive process controlled by two parameters: an error sensitivity (controls the amount of learning from error) and a retention factor (controls the amount of decay).

To determine if the savings we observed following gradual adaptation was due to changes in error-based learning or forgetting, we fit state-space models to individual participant learning

curves during the second rotation periods in all 3 gradual adaptation groups (Fig. 4A, green, blue, and magenta). To obtain naïve learning parameter estimates, we fit the state-space model to the initial abrupt adaptation period in the control group in Fig. 1 (Fig. 4A, black).

To determine if the initial gradual adaptation and subsequent washout period altered the stability of the motor memory during the readaptation period, we compared retention factors across all 4 groups (Fig. 4B). We did not observe a statistically significant change in retention after exposure to the gradual rotation (one-way ANOVA, $F(3,36)=0.2$, $p=0.895$).

To determine if instead, a change in error sensitivity boosted adaptation rates during the second exposure period, we compared the state-space model error sensitivity parameters across all 4 groups (Fig. 4C). As in past studies[11,16,22], prior adaptation did alter the sensitivity to error during the second exposure (one-way ANOVA, $F(3,36)=3.81$, $p=0.0181$), accelerating re-learning rate (Fig. 3D). Interestingly, we found a statistically significant increase in error sensitivity over naïve, in the no-feedback condition (post-hoc Dunnett's test, $p=0.0387$), but not in the abrupt condition (post-hoc Dunnett's test, $p=0.897$). In the gradual washout condition, we observed a trend towards an increase in error sensitivity over the naïve condition, though this trend did not reach statistical significance (post-hoc Dunnett's test, $p=0.548$).

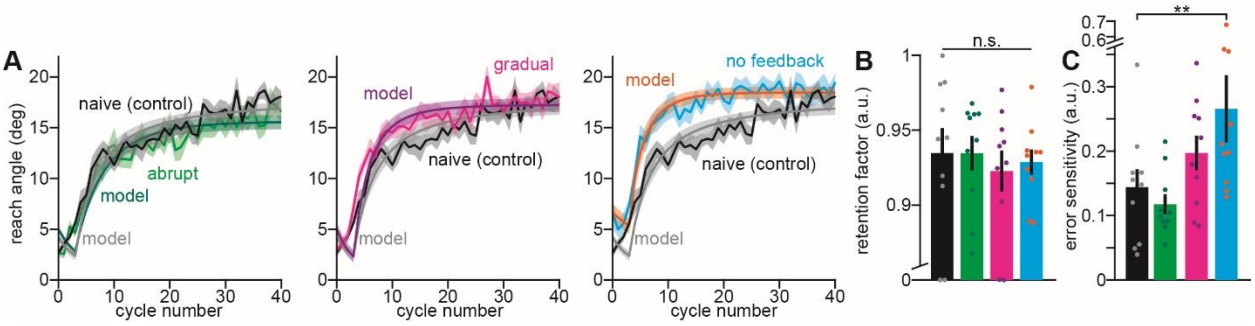

Figure 4. Savings after gradual learning is mediated by an increase in error sensitivity. **A.** Learning curves and visualization of savings. The reach angle at maximum velocity was calculated on each trial and averaged within each 4-trial cycle. Each inset compares naïve adaptation (control, black) to 1 of 3 groups that experienced an initial gradual rotation and secondary abrupt rotation, separated by washout (left: gradual group that de-adapted with abrupt removal of the rotation, middle: gradual group that de-adapted with gradual removal of the rotation, right: gradual group that de-adapted with any visual error). We fit a state-space learning model (model) to individual participant reach angles that describes learning as a recursive trial-to-trial process of error-based adaptation and decay. **B.** Comparison of retention factors. Retention factors estimated by state-space model fits are compared across the secondary abrupt learning periods of the gradual group and the initial naïve adaptation period in the control group. **C.** Comparison of error sensitivity. The sensitivity to error parameters estimated by state-space model fits are compared across the secondary abrupt learning periods of the gradual group and the initial naïve adaptation period in the control group. Errors bars indicated mean ± 1 standard error of the mean. Single points in **B** and **C** represent individual participants. Statistics: n.s. indicates $p > 0.05$, ** indicates $p < 0.01$.

Taken together, this indicates that initial gradual adaptation elevates sensitivity to error, leading to savings. However, errors experienced during the washout phase can reverse this gain in error sensitivity. Enhancement in error sensitivity is optimally preserved when visual errors are totally removed in the washout phase via a no-feedback condition.

Discussion

The conditions necessary to increase the learning rate of the sensorimotor system are not completely known. This is clearly illustrated in gradual adaptation paradigms where participants

397 adapt to a perturbation slowly and are then re-tested in an abrupt context following a period of
398 washout. Whereas some studies have observed more rapid learning in this context[23,26], other
399 accounts have found that gradual learning is unable to improve abrupt adaptation[24]. Here we
400 considered whether this contradiction might be due to variations in the de-adaptation phase that
401 separates two learning periods in typical savings paradigms. Specifically, does the salience of
402 oppositely-signed errors during washout inhibit savings after gradual learning?

403 Here we examined this idea by altering the type of error experienced during the washout
404 phase after a gradual adaptation period. We considered no-feedback, gradual, and abrupt de-
405 adaptation conditions that differ along the following error size gradient. (1) Removing visual
406 feedback eliminates visuomotor error completely, and so adaptation decays only due to a
407 forgetting process[32]. (2) With gradual de-adaptation, errors are present, but are small because
408 the motor action and perturbation are reduced in tandem preventing the occurrence of large
409 errors. (3) Similar to abrupt adaptation, abrupt de-adaptation results in the largest errors due to
410 the immediate removal of the perturbation when subjects still remain in the fully adapted state.
411 Our empirical analyses revealed accelerated learning after subjects de-adapted gradually or
412 without feedback, but not after abrupt removal of the initial perturbation (Fig. 3D). Interpreted
413 in an error-based framework, this suggests that the size of oppositely-signed errors during the
414 washout phase is inversely related to the propensity to save: larger errors appear to nullify
415 potential improvements in learning following initial gradual adaptation.

416 This conclusion qualitatively aligns with previous work by Kojima et al. (2004)[9], which
417 demonstrated that savings in the oculomotor system is sensitive to the duration of washout:
418 when the duration of the washout phase is increased, the learning rate during the re-exposure

419 phase reverts to its baseline state, abolishing savings. Thus, both the duration of error
420 presentation and the error magnitude during washout seem to negatively interact with the
421 expression of savings. This hypothesis may help to explain the mixed results noted above in
422 visuomotor studies of gradual learning. Both Coltman et al. (2021)[26] and Yin & Wei (2020)[23]
423 employed shorter washout periods, and observed savings following gradual adaptation, whereas
424 Herzfeld et al. (2014)[24] applied a longer washout period and did not find savings after gradual
425 learning. This possible explanation could easily be tested in a follow-up study that varies the
426 length of the washout period after an initial gradual learning period.

427 Along these lines, Kitago et al. (2013)[32] anecdotally noted that increasing the number of
428 washout trials appeared to dampen the magnitude of savings relative to earlier studies that
429 applied much fewer de-adaptation trials[33,34]. With that said, their observation was made in the
430 context of an abrupt-then-abrupt savings protocol, instead of the mixed gradual-then-abrupt
431 design we used. The expression of savings following abrupt or gradual learning periods may have
432 critical differences. That is, whereas removing feedback after gradual learning resulted in rapid
433 adaptation in our study, it abolished savings after abrupt learning in the experimental conditions
434 used by Kitago et al. (2013)[32]. We think that this stark discrepancy is likely caused by variations
435 in the utilization of implicit and explicit learning processes, which were not directly measured by
436 Kitago et al., nor in our current study. That is, gradual learning paradigms reduce the size of error,
437 which in turn limits cognitive awareness of the perturbation and associated strategic re-aiming
438 strategies[22,23,35]. We also anticipate larger strategy use in the Kitago et al.'s study due to the
439 utilization of a single target (as opposed to the 4 targets used herein), which also appears to
440 attenuate procedural aftereffects[36,37]. Accordingly, savings in gradual-then-abrupt learning

441 paradigms have been linked to increases in implicit learning rates[23], as opposed to overt
442 strategies that tend to dominate savings responses in abrupt-then-abrupt protocols[7,12]. Thus, we
443 hypothesize that washout has divergent effects on the ability of implicit and explicit systems to
444 save: removing feedback during washout may protect savings in the implicit system (which might
445 otherwise be suppressed by "negatively-signed" errors during the washout period[38]), but
446 negatively impact savings in the explicit system. This fascinating possibility could be tested in
447 follow-up studies that assay implicit and explicit contributions to learning following abrupt and
448 gradual adaptations with differing washout conditions.

449 To understand what learning property links washout to the capacity to save, we applied
450 a state-space model that casts short-term adaptation as a cumulative process of trial-to-trial
451 error-based learning and decay. This model indicated that gradual savings appears to involve an
452 upregulation in sensitivity to error, that is reversed by exposure to large errors in the washout
453 phase (Fig. 4C). This outcome comports with past work, suggesting that increases in error
454 sensitivity are the primary source of accelerated re-learning after abrupt, gradual, or random
455 perturbations[26], and the adaptation of disparate motor systems such as reaching[16,22,26] and
456 walking[11]. Thus, a growing body of evidence suggests that exposure to a perturbation causes an
457 increase in error sensitivity that can improve performance in subsequent exposures to similar
458 perturbations[22,24]. Our results suggest that increases in error sensitivity can be undermined by
459 inconsistently signed errors experienced in between learning periods.

460 What specific properties of error suppress previous gains in error sensitivity? We found
461 that error sensitivity was elevated specifically in individuals that de-adapted without feedback,
462 suggesting that improvements in error sensitivity can be protected by the absence of error. With

463 that said, given that the subjects' re-learning rates were similarly increased in both no-feedback
464 and gradual de-adaptation conditions (Fig. 3D), it is possible that error sensitivity was also
465 elevated in the gradual de-adaptation group (consistent with the trend in Fig. 4C), but that we
466 did not have sufficient statistical power to detect this effect. Thus, it is not currently clear
467 whether error sensitivity is reduced by the experience of *any* opposing error, or whether the size
468 of the opposing error further modulates the rate of error sensitivity decline.

469 Our findings have critical implications for the learning rules suggested by an influential
470 error sensitivity model defined by a memory of errors[13,24,25]. The memory of errors model that
471 was initially proposed by Herzfeld et al. (2014)[24] accounts for changes in error sensitivity based
472 on the statistical properties of error. Namely, when errors have consistent signs, this indicates
473 that the learning system could have adapted more to the initial experience of error to better
474 eliminate performance error. A critical feature of this model is its locality: changes in error
475 sensitivity are restricted to errors of a given size. In other words, the experience of consistently
476 small or large errors modulates error sensitivity specific to errors of that magnitude. Thus,
477 contrary to our findings, a memory of errors model predicts that a gradual adaptation paradigm
478 will not lead to savings during an abrupt perturbation, because abrupt errors are much larger
479 than those experienced during a gradual perturbation. Thus, our results add to a growing body
480 of evidence[23,26] suggesting a need to revisit properties of the error sensitivity landscape; it may
481 be that the experience of consistent errors generalizes more broadly to unexperienced errors of
482 disparate sizes than previously appreciated.

483 The possibility that changes in error sensitivity extend beyond the experienced range of
484 errors could help not only to understand patterns of adaptation in gradual-then-abrupt learning

485 paradigms, but also suppression of learning rates in anterograde interference paradigms[22,31,39–
486 41]. That is, whereas increases in error sensitivity have been linked to improvements in learning
487 when two similar perturbations are experienced in sequence, decreases in error sensitivity have
488 been found to produce a slowing of adaptation when transitioning between two contrasting
489 perturbations[31]. To date, no memory of errors model has attempted to integrate these opposing
490 error sensitivity-driven effects on learning rate. Limited application of the memory of errors
491 model to interference paradigms arises, because learning in response to "positively-signed"
492 errors during the first exposure does not produce error sensitivity changes that generalize to
493 "negatively-signed" errors during the second exposure (as they have not been experienced
494 before). Our findings, that large oppositely-signed errors during washout reverse prior
495 enhancements in error sensitivity (Fig. 4C), suggest that the experience of a sensorimotor error
496 produces two distinct effects: (1) an increase in sensitivity to similar errors, and (2) a suppression
497 in error sensitivity to contrasting errors. This second suppressive learning property may be a
498 critical process missing from current memory of errors models that would aid in interpreting both
499 the dissolution of savings following certain types of washout, as well as interference effects.

500 We speculate that this antagonistic interaction between the response to "positive" and
501 "negative" errors may be encoded within cerebellar learning circuits that mediate error-based
502 learning processes, a structure known to encode error directionality based on its anatomical
503 connections with the inferior olive[42–44]. In particular, errors of a given direction (*i.e.*, sign) lead to
504 complex spiking in some Purkinje-cell (P-cell) subpopulations in the cerebellar cortex, and
505 suppression in others. Complex spiking events in turn lead to long term potentiation or
506 depression at P-cell synapses with parallel fibers[45]. While it is not clear precisely how error

507 sensitivity is encoded by groups of P-cells, our findings suggest the possibility that prolonged
508 absence of complex spikes (when errors are opposite of the preferred direction) during washout
509 periods may produce cellular or synaptic-level changes that reduce the plastic learning potential
510 of these neurons in the future (*i.e.*, during the re-exposure period). This idea, and the source of
511 cerebellar error sensitivity more generally, remain to be examined.

512 It is important to distinguish this memory of errors framework from that of Bayesian
513 inference models that incorporate both error-based learning processes and inference across
514 multiple sensorimotor contexts[46,47]. In single-context memory of errors models, the same
515 adaptive states apply uniformly across different experimental periods, such that any change in
516 learning rate must be due to a variation in learning parameters: sensitivity to error or memory
517 retention. But with multiple contexts, as in the Bayesian COIN model by Heald et al. (2021)[46], the
518 apparent learning rate is influenced by inferring which context is most likely given sensory
519 information. For the COIN model, visuomotor adaptation involves two contexts: a baseline
520 context and a rotation context. Faster learning during the second exposure is caused not by a
521 change in the response to error, but by an increase in the propensity to expect the rotation given
522 prior training during the initial exposure period. Thus, our findings could have important
523 implications for how this inference occurs in the sensorimotor system. Namely, the errors (*i.e.*,
524 sensory information) experienced during the washout period alters the inference process: with
525 large "negatively-signed" errors during the washout period, the nervous system decreases its
526 expectation that the rotation state (with its "positively-signed" errors) will occur again in the
527 future. This idea, and a broader comparison between the memory of errors and Bayesian
528 frameworks on the effects of washout on future learning, remain to be tested.

Competing interests

The authors declare no competing interests.

Data availability

All data and analysis code will be made accessible via OSF upon acceptance.

Author contributions

MJ, BM and JW designed the experiments and methodology. MJ and BM collected data. MJ and STA analyzed data and created figures. MJ and STA wrote manuscript. MJ, STA, and JW edited that manuscript.

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