Re-exposure to a sensorimotor perturbation produces opposite effects on explicit and implicit learning processes

Short title: Implicit adaptation is attenuated upon re-learning

Guy Avraham[1,2]*, J Ryan Morehead[3,4], Hyosub E Kim[5], Richard B Ivry[1,2]

1. Department of Psychology, University of California, Berkeley, Berkeley, CA 94720, USA

2. Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA 94720, USA

3. School of Psychology, University of Leeds, Leeds, LS2 9JT, United Kingdom

4. John A. Paulson School of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138, USA

5. Department of Physical Therapy, University of Delaware, Newark, DE 19716, USA

* Corresponding author

E-mail: guyavraham@berkeley.edu

Abstract

The motor system demonstrates an exquisite ability to adapt to changes in the environment, and to quickly reset when these changes prove transient. If similar environmental changes are encountered in the future, learning may be faster, a phenomenon known as savings. In studies of sensorimotor learning, a central component of savings is attributed to the explicit recall of the task structure and appropriate compensatory strategies. Whether implicit adaptation also contributes to savings remains subject to debate (Leow et al., 2020; Yin and Wei, 2020). We tackled this question by measuring, in parallel, explicit and implicit adaptive responses in a visuomotor rotation task, employing a protocol that typically elicits savings. While the initial rate of learning was faster in the second exposure to the perturbation, an analysis decomposing the two processes showed the benefit to be solely associated with explicit re-aiming. Surprisingly, we found a significant decrease after relearning in aftereffect magnitudes during no-feedback trials, a direct measure of implicit adaptation. In a second experiment, we isolated implicit adaptation using clamped visual feedback, a method known to eliminate the contribution of explicit learning processes. Consistent with the results of the first experiment, participants exhibited a marked reduction in the adaptation function, as well as an attenuated aftereffect when re-learning from the clamped feedback. Motivated by these results, we re-analyzed data from prior studies and observed a consistent, yet unappreciated pattern of attenuation of implicit adaptation during relearning. These results indicate that explicit and implicit sensorimotor processes exhibit opposite effects upon relearning: Explicit learning shows savings, while implicit adaptation becomes attenuated.

Introduction

Throughout the life span, the motor system needs to learn to correct for errors that emerge due to changes in the state of the body and the environment. When re-experiencing a familiar change,

learning can be faster, a phenomenon known as savings upon relearning (Ebbinghaus, 1913; Huang et al., 2011; Krakauer et al., 2005; Mawase et al., 2014). Constraints on the computations underlying savings in sensorimotor learning have been the subject of considerable debate (Berniker and Kording, 2011; Herzfeld et al., 2014; Smith et al., 2006; Zarahn et al., 2008). Recently, converging lines of evidence from visuomotor adaptation tasks indicate that a central component of savings reflects improvement in the use of explicit strategies to counteract an imposed perturbation (Haith et al., 2015; Huberdeau et al., 2015; Leow et al., 2020; Morehead et al., 2015). That is, when participants first encounter a visual perturbation (e.g., rotation of the visual feedback), they may learn to explicitly adjust their behavior to compensate for the perturbation (e.g., aim in the opposite direction of the rotation). Later, upon re-exposure to the same perturbation, people quickly recall a successful strategy that had been previously employed, resulting in faster learning.

Yet, the behavioral changes observed during sensorimotor learning do not arise solely from explicit strategy use. The behavioral change in such tasks is also driven by implicit adaptation, the adjustment in the sensorimotor map that occurs outside awareness and volitional control (Kim et al., 2020). Indeed, in many contexts, especially those involving small perturbations, most of the learning is implicit (Bond and Taylor, 2015; Kagerer et al., 1997; Morehead et al., 2015). Whether and how implicit adaptation contributes to savings remains unclear: While some studies have proposed that faster relearning is attributed to implicit processes (Coltman et al., 2019; Herzfeld et al., 2014; Yin and Wei, 2020), others reported no change in the rate of implicit adaptation upon relearning (Haith et al., 2015; Leow et al., 2020; Morehead et al., 2015). Importantly, it can be difficult to obtain a clean assessment of the time course of implicit adaptation across multiple experimental blocks given potential influences from explicit processes and the extended resilience of adaptation over time (Hadjiosif and Smith, 2013).

Here, we take advantage of protocols specifically designed to isolate explicit and implicit learning processes, asking whether each process is subject to savings upon relearning. We employed a savings design where the same perturbation was imposed during two epochs, separated by a washout block that allowed sufficient number of reaches in the absence of the perturbation for the adaptive response to be unlearned (Krakauer et al., 2005; Zarahn et al., 2008). In Experiment 1, the visual feedback was rotated by 45°, and by manipulating the instructions, we obtained separate estimates of explicit aiming and implicit adaptation (Morehead et al., 2015). In Experiment 2, we used task-irrelevant clamped visual feedback to isolate performance changes resulting from implicit adaptation (Morehead et al., 2017). The results revealed opposite effects on explicit and implicit motor processes upon relearning: While explicit strategy use improved in response to the second exposure of the perturbation, implicit adaptation was attenuated. A review of the literature and re-analysis of several studies revealed prior, yet unappreciated, evidence that implicit adaptation not only fails to exhibit savings, but actually becomes attenuated in response to previously experienced errors.

Results

In Experiment 1, we assessed the contributions of explicit and implicit motor learning processes to savings. Following a baseline block with veridical visual feedback, participants were exposed to the first learning block in which, on Rotation trials, the visual feedback cursor was rotated 45° with respect to the position of the hand (Fig. 1A). Participants were cued about the perturbed feedback and instructed that their task was to “move the cursor to the target” (Rotation 1). The compensatory response on Rotation trials with this manipulation involves both explicit and implicit processes (Morehead et al., 2015; Taylor et al., 2014). On a set of randomly selected interleaved trials, the feedback was eliminated, and the participants were instructed to aim directly to the target (Probe 1 trials), with the instructions emphasizing that they should stop using any strategy

employed on the Rotation trials. These Probe trials are designed to assay the state of implicit adaptation (Huberdeau et al., 2019; Morehead et al., 2015; Vandevoorde and Orban de Xivry, 2019).

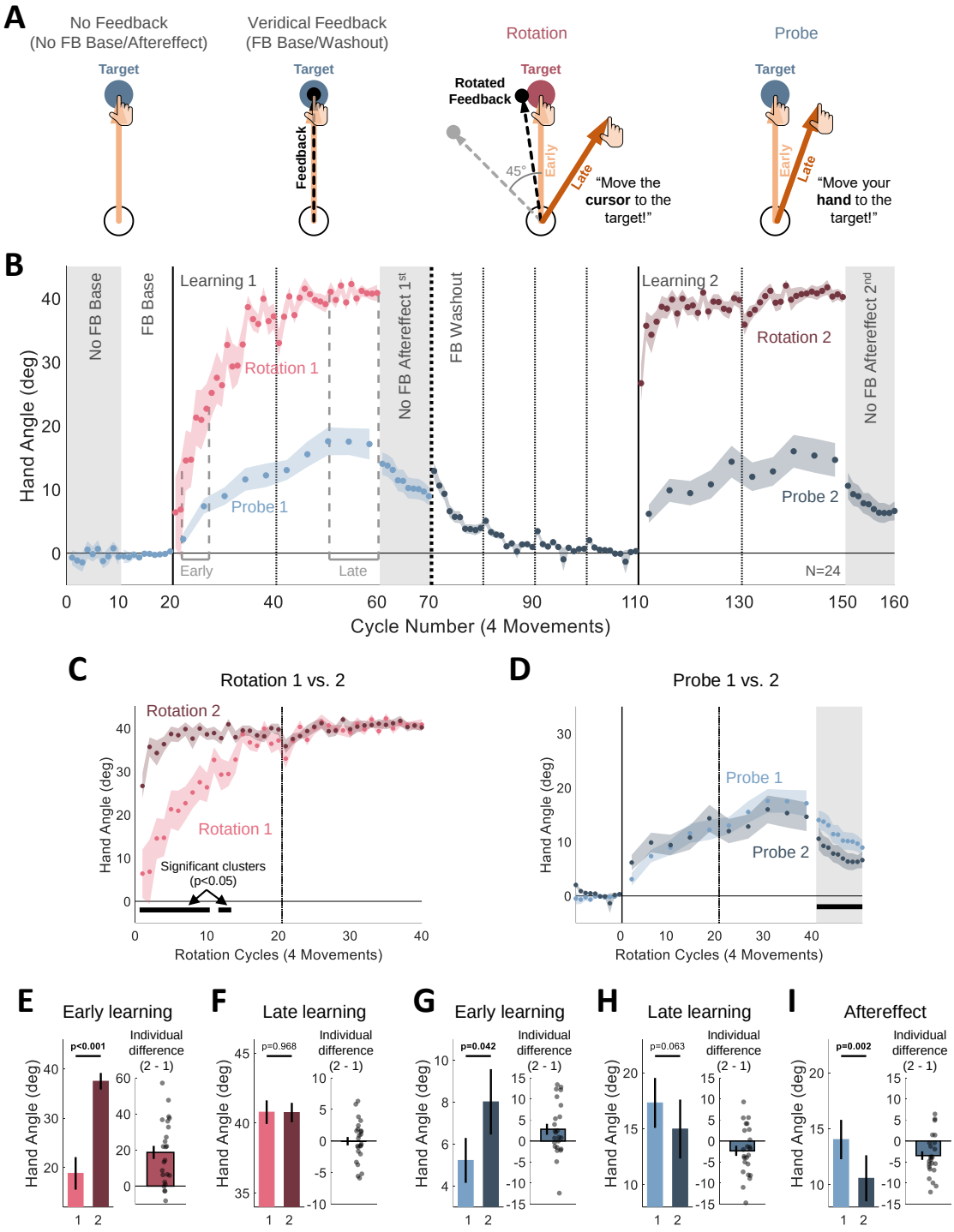


Figure 1. Experiment 1: Upon relearning a visuomotor rotation, explicit strategies show savings while implicit adaptation is attenuated.

(**A**) Task-level schematics of all trial types. (**B**) Time course of mean hand angle averaged over cycles (4 movements) when participants (N=24) were asked to aim for the target (blue), either during No Feedback blocks (No FB Baseline and Aftereffect, gray background), Veridical Feedback blocks (FB Baseline and Washout), or no feedback Probe trials, and when asked to compensate for a rotated cursor (Rotation, pink). Light and dark colors signify blocks 1 and 2 of the experiment. Dotted vertical lines denote one (thin) and two (thick) min breaks. The labels 'Early' and 'Late' mark the cycles used for operationalizing measures of early and late learning. (**C**, **D**) To highlight changes across blocks, overlaid hand angle functions of blocks 1 and 2 for overall learning (explicit and implicit, Rotation trials, *C*) and implicit adaptation (Baseline, Probe and Aftereffect trials, *D*). Horizontal thick black lines mark clusters of cycles that show significant difference between the blocks with $p<0.05$ probability. Cycle numbers in both *C* and *D* correspond to the cycles of the Rotation trials. (**E-I**) Summary analysis of Early learning (*E*, *G*) and Late learning (*F*, *H*) for the Rotation (*E*, *F*) and Probe (*G*, *H*) conditions, and of the aftereffects (*I*). Left pair of bars show the mean across participants for each block, and right bar shows the mean of the within-participant differences (Block 2 – Block 1). Black dots indicate individual difference scores. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

On Rotation trials, the participants' hands deviated in the direction opposite to the rotation, approaching the ideal 45° change in hand angle by the end of the block ([mean ± SEM], 40.8°±0.84°, Fig. 1B). On Probe trials, the hand angle was also shifted in the same direction, despite instructions to reach directly to the target. By the end of the learning block, this shift was markedly less than that observed on the Rotation trials (17.3°±2.23°, $t(23)=-8.56$, $p<0.001$, $BF_{10}=9.91*10^5$, $d=-1.75$). The large difference in hand angle between the Rotation and Probe trials is consistent with the assumption that the participants employed an explicit aiming strategy

to achieve good performance on the Rotation trials and followed the instructions to stop using this strategy on Probe trials (Fig. S1).

Following an extended washout with veridical feedback, the participants experienced a second learning block, again composed of trials with perturbed feedback (Rotation 2), interspersed with no feedback trials (Probe 2).

Marked savings was observed on the Rotation trials: Performance improved at a faster rate relative to the first learning block (Fig. 1C). To statistically evaluate the locus of savings, we performed a series of analyses on the Rotation and Probe trials. For each trial type, two approaches were employed. The first, following conventions in the literature, was designed to focus on differences between the two learning blocks at predefined stages (Krakauer et al., 2005; Leow et al., 2020): Early (cycles 3-7 of each learning block) and Late (last 10 cycles). Here we used a 2 (Stage: Early vs Late) x 2 (Block: Learning 1 vs Learning 2) repeated measures ANOVA, with planned comparisons targeted at the differences between blocks. In the second analysis, we used a cluster-based permutation test to identify clusters of consecutive cycles that show a significant difference between the two learning blocks without relying on predefined assumptions about specific cycles (Labruna et al., 2019; Maris and Oostenveld, 2007).

Considering first the data from the Rotation trials, the ANOVA showed main effects of learning within each block (Stage: $F(1,23)=51.4$, $p<0.001$, $\eta_p^2=0.53$) and savings across blocks (Block: $F(1,23)=26.2$, $p<0.001$, $\eta_p^2=0.69$). The interaction was also significant (Stage x Block interaction: $F(1,23)=25.4$, $p<0.001$, $\eta_p^2=0.52$). The increase between blocks, the savings effect, was significant in the early stage ([mean difference ± SEM], 18.7°±3.62°, $t(23)=5.16$, $p<0.001$, $BF_{10}=775$, $d=1.05$, Fig. 1E), but not in the late stage where performance was near asymptote (0.03°±0.67°, $t(23)=-0.04$, $p=0.968$, $BF_{10}=0.215$, $d=-0.01$, Fig. 1F). The cluster analysis revealed that the shift in hand direction was larger in the first quarter of the Rotation trials during the

relearning block, relative to first learning block ($p<0.05$, Fig. 1C), consistent with the pre-defined analysis.

A more complex pattern was observed when analyzing the Probe trials (Fig. 1D). In the pre-defined stage analysis, hand angle increased within each block, indicative of the operation of implicit adaptation (Stage main effect: $F(1,23)=45.0$, $p<0.001$, $\eta_p^2=0.66$). However, the effect of block was not significant ($F(1,23)=0.07$, $p=0.800$, $\eta_p^2=0.00$). This null result is consistent with the proposition that implicit adaptation does not contribute to savings (see Morehead et al., 2015). This conclusion, however, is qualified by a significant interaction ($F(1,23)=8.30$, $p=0.008$, $\eta_p^2=0.27$): The change in hand angle was slightly faster in the early stage of the second learning block (2.79°±1.30°, $t(23)=2.15$, $p=0.042$, $BF_{10}=1.49$, $d=0.44$, Fig. 1G), but marginally smaller for the late stage (-2.34°±1.20°, $t(23)=-1.96$, $p=0.063$, $BF_{10}=1.09$, $d=-0.40$, Fig. 1H). In the cluster analysis, no significant difference was found between the learning blocks.

Although reaction time was not emphasized in this study, these data also point to a dissociation between explicit and implicit processes in savings. Reaction times were smaller on Rotation 2 (695±46 ms) compared to Rotation 1 (858±74 ms) trials ($t(23)=-2.93$, $p=0.007$, $BF_{10}=6.21$, $d=-0.60$). This decrease is consistent with the idea that strategy use and/or strategy recall improve with experience (McDougle and Taylor, 2019). In contrast, reaction times did not vary between the first (667±28 ms) and second (667±39 ms) learning blocks for the Probe trials ($t(23)=0.008$, $p=0.993$, $BF_{10}=0.215$, $d=0.00$).

The aftereffect data provide a second measure of implicit learning. Here the visual feedback was withheld, and the participants were reminded to reach directly to the target. Indeed, these data provide a cleaner measure if we assume participants may occasionally lapse in switching their behavior between the Rotation and Probe trials (see below, Rogers and Monsell, 1995). Surprisingly, the aftereffect was weaker after the second block compared to the first in a predefined analysis restricted to the first cycle of each aftereffect block (-3.47°±1.01°, $t(23)=-3.43$,

$p=0.002$, $BF_{10}=17.2$, $d=-0.70$, Fig. 1I), consistent with the trend observed above for the late stage of the learning blocks. Moreover, the cluster analysis showed a significant reduction of hand angle across the entire second aftereffect block ($p<0.05$).

To summarize, the results of Experiment 1 show differential effects of relearning on explicit and implicit processes. Clear evidence of savings was observed on the Rotation trials, evident in the early trials where the largest component to learning comes from the use of an explicit aiming strategy (Haith et al., 2015; Morehead et al., 2015). In contrast, the overall behavior on the Probe trials was quite comparable between the blocks. There was a modest increase in hand angle early on in the second learning block relative to the first block which might be indicative of savings. However, the design required participants to frequently switch between aiming away from the target (Rotation trials) to aiming to the target (Probe trials). Since the change in aiming is larger during the second learning block, any failure to completely dispense with the aiming strategy would contaminate the Probe trials in a way that would make it appear as if they exhibit savings. Indeed, late in learning, where the behavior on Rotation trials has reached asymptote on both blocks, the difference in hand angle on the Probe trials was actually numerically lower than on the first block.

Importantly, the aftereffect data point to a robust attenuation of implicit adaptation upon re-exposure to a perturbation. We considered if this surprising attenuation might be an artifact of the experimental design, and in particular effects that may occur with the transition between the learning and aftereffect blocks. First, implicit learning is known to involve both labile and stable components, with the former manifest by a reduction in the aftereffect by around 25% over a ~60 s delay, even in the absence of any movement (Hadjiosif et al., 2014). Thus, the attenuation could result from differences in the labile component between the first and second blocks. However, the amount of elapsed time between the end of each learning block and the completion of the first cycle of the aftereffect block was similar for the first and second learning phases. There was a

break of approximately 10 s prior to the start of the aftereffect block (during which the experimenter provided the new instructions), and the first cycle of the aftereffect block took about 13 s to complete (Aftereffect 1: 13.6±1.7 s; Aftereffect 2: 12.4±1.7 s; t(23)=-0.710, p=0.485, BF_{10}=0.270, d=-0.15). Thus, the contribution from the labile component should be similar for the two aftereffect blocks.

Second, estimates of implicit adaptation can be affected by differential use in aiming (Day et al., 2016). Prior studies have shown that the generalization function of implicit adaptation is centered at the aiming location. As such, the increase in aiming in the second block could distort the estimate of adaptation in the aftereffect block since the measurements in this block are obtained for reaches to the target location. The mean hand angle in the late phase of the Probe trials are ~2° lower on the second learning block. Given that the hand angle is the same on the Rotation trials, this would imply that the aiming location is shifted ~2° farther from the target in the second block. Based on estimates of Gaussian generalization functions in the literature (e.g., McDougle et al., 2017), a 2° difference in aiming would be expected to produce a miniscule reduction in the aftereffect, ~0.5°, or only 14% of the observed reduction in Aftereffect 2. We recognize that this is a crude estimate given that aiming strategy changes over experience and we do not know the dynamics of aim-based generalization. Despite this limitation, it seems highly unlikely that the reduced aftereffect in the second learning block is due to changes in aiming location.

To obtain a purer assay of the effect of relearning upon implicit adaptation we conducted a second experiment using a method thought to entirely eliminate changes in aiming and thus avoid issues with switching and generalization. Instead of presenting the feedback at a position contingent on the hand position, Experiment 2 used task-irrelevant clamped feedback (Morehead et al., 2017). On each reach during the learning blocks (Clamp 1 and Clamp 2), the visual feedback followed a fixed path, rotated 15° (either clockwise or counterclockwise, fixed for a given participant) from the target, with the radial position matched to the participants' hand (Fig. 2A). The participant was

informed that the angular position of the cursor would be independent of her hand position and that she should ignore the feedback, always reaching directly to the target. Given these instructions, changes in hand angle in response to task-irrelevant clamped feedback is assumed to be implicit, an inference supported by converging evidence from various measures of adaptation (Morehead et al., 2017; Jonathan S. Tsay et al., 2020d).

The main group of participants (Test group) experienced the clamped feedback over two learning blocks, separated by an extended washout block (Fig. 2B). As expected, participants showed a robust adaptation effect in both learning blocks, with the heading direction of the hand movement drifting away from the target in the opposite direction of the feedback (Fig. 2C). The presumption that this change in behavior was implicit is supported by a number of observations. First, there is a close match between the magnitude of hand angle at the end of the learning block and start of the aftereffect block ([mean Aftereffect/Late learning, 95% confidence interval (CI)], Learning 1: [mean, 95% CI], 0.94, [0.88 1.00], Learning 2: 0.85, [0.74 0.96]). The small decay is likely due to some forgetting during the short break between these blocks (Hadjiosif and Smith, 2013; Hadjiosif et al., 2014; Zhou et al., 2017). Second, consistent with the hypothesis that participants aimed directly to the target throughout the experiment, reaction times were uniformly fast (~400 ms) and comparable across different phases of the experiment (Clamp vs Aftereffect: $t(15)=0.810$, $p=0.430$, $BF_{10}=0.340$, $d=0.20$; Learning 1 vs Learning 2: $t(15)=-0.390$, $p=0.702$, $BF_{10}=0.273$, $d=-0.10$). Third, in a debriefing survey, all of the participants reported that they always planned their reaches to the target and none reported awareness of the systematic changes in hand direction.

We used the same two-part statistical analysis as in Experiment 1, first analyzing the data from pre-specified blocks and then with the cluster analysis that considers all of the data. The ANOVA showed a main effect of stage ($F(1,15)=53.4$, $p<0.001$, $\eta_p^2=0.78$), with hand angle increasing between the early and late phases of a block. Importantly, the effect of block was also significant ($F(1,15)=10.8$, $p=0.005$, $\eta_p^2=0.42$), with the adaptation function markedly attenuated in the second

learning block (Fig 2D). Although the interaction was not significant ($F(1,15)=0.76$, $p=0.399$, $\eta_p^2=0.05$), we conducted our planned comparisons for each learning stage. In the early phase, adaptation was numerically lower, but the difference was not significant ([mean difference ± SEM], -1.82°±1.33°, $t(15)=-1.37$, $p=0.191$, $BF_{10}=0.562$, $d=-0.34$, Fig. 2E). In the late phase, the attenuation of adaptation was significant (-3.28°±0.91°, $t(15)=-3.59$, $p=0.003$, $BF_{10}=16.3$, $d=-0.90$, Fig. 2F). A significant attenuation effect was also found in the planned comparison of the aftereffect data (-5.00°±1.34°, $t(15)=-3.74$, $p=0.002$, $BF_{10}=21.5$, $d=-0.94$, Fig. 2G). The cluster analysis provided a similar picture. Implicit adaptation was attenuated throughout much of the learning and aftereffect blocks ($p<0.05$, Fig. 2D).

Given that attenuation of implicit adaption in re-learning has not been highlighted in the literature, we conducted a replication study using an online platform (Jonathan S. Tsay et al., 2020a), one in which the crowdsourced participants complete the study remotely using their individual display and response devices. The results from the online study were quite similar to those observed in Experiment 2 (Fig S2, all statistics are reported in the caption). Of particular note, adaptation was lower during the second block in the late phase of learning ([mean difference ± SEM], -1.57°±0.74°, $t(47)=-2.14$, $p=0.038$, $BF_{10}=1.25$, $d=-0.31$) and in the aftereffect (-3.35°±0.81°, $t(47)=-4.14$, $p<0.001$, $BF_{10}=168$, $d=-0.60$), and the attenuation was observed in multiple clusters throughout the learning and aftereffect blocks ($p<0.05$). Considered in tandem with the results of Experiment 2, the results clearly show that implicit adaptation elicited in response to clamped feedback is attenuated upon relearning.

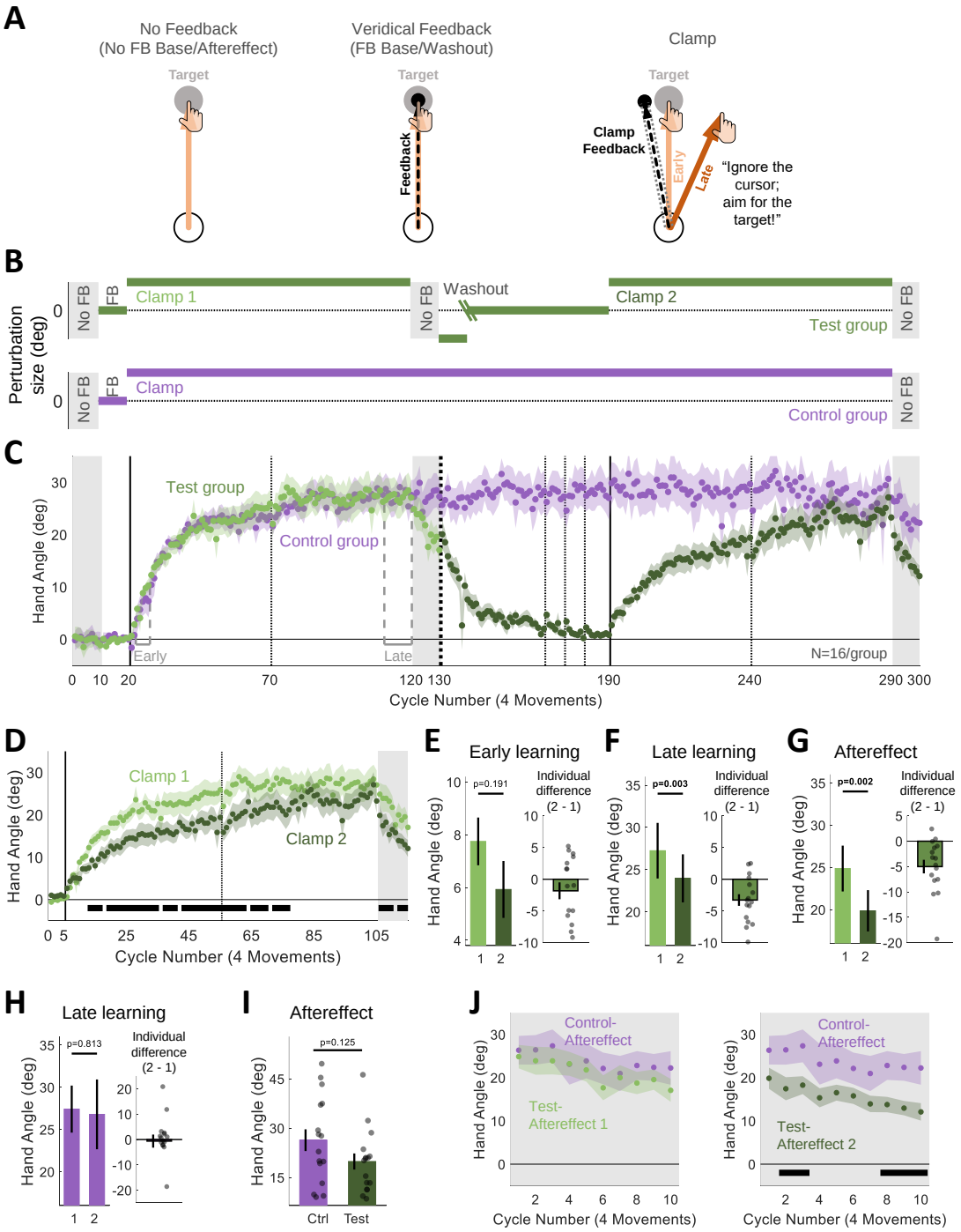


Figure 2. Experiment 2: Task-irrelevant clamped feedback revealed an overall attenuation of implicit adaptation upon relearning.

(**A**) Task-level schematics of all trial types. (**B**) Experimental protocol of two experimental groups: Test (N=16, green) and Control (N=16, purple). For the Test group, the green oblique lines in the Washout block

represent a transition from a reversed-clamp phase to a veridical feedback phase; the cycle of the transition was determined based on each individual's performance in the reversed-clamp phase (see Methods). (**C**) Time courses of mean hand angle averaged over cycles (4 movements) for both groups. For the Test group, light and dark green colors signify blocks 1 and 2 of the experiment, with the onset of the task-irrelevant clamped feedback marked by the vertical solid lines. Dotted vertical lines denote one (thin) and two (thick) min breaks. The labels 'Early' and 'Late' mark the cycles used for operationalizing measures of early and late learning. (**D**) Overlaid hand angle functions for the two blocks. Horizontal thick black lines denote clusters that show a significant difference between blocks 1 and 2 ($p<0.05$). (**E-H**) Summary analysis of Early learning (*E*), Late learning (*F*) and Aftereffect (*G*) stages for the Test group, and Late learning for the Control group (*H*). Left pair of bars show the mean across participants for each block, and right bar shows the mean of the within participant differences Block 2 – Block 1. Black dots indicate individual difference scores. (**I**) Summary analysis comparing the Aftereffect between the groups in the last No FB block. Black dots represent data of individual participants. (**J**) Overlaid hand angle functions for the Aftereffect block of the Control group and the Aftereffect 1 (left panel) or Aftereffect 2 (right panel) of the Test group. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

We considered the possibility that the attenuation might reflect fatigue or some sort of a habituation process, one in which the response to the clamped error signal becomes attenuated with extended use. To test this hypothesis, a separate group of participants (Control group) was exposed to a single, extended block of clamped feedback with no washout (Fig. 2B). The participants from this group showed near-identical adaptation to that observed in the Test group over the cycles corresponding to the first learning block (Fig. 2C). Moreover, they remained at this asymptote for the remainder of the experiment, with no indication of a shift in hand angle back towards the target. This was confirmed in an analysis comparing the hand angle for the Control group at cycles corresponding to the late stages for the first and second learning blocks in the

Test group (cycles 111-120 vs cycles 281-290, -0.62°±2.58°, t(15)=-0.24, p=0.813, BF_{10}=0.262, d=-0.06, Fig. 2H).

Finally, we performed a direct comparison of the aftereffect data from the Test and Control groups. In the pre-defined analysis (cycle 291 only), the magnitude of the aftereffect was ~25% lower in the Test group (19.9°±2.45°) than in the Control group (26.4°±3.31°), although this difference was not significant (t(30)=-1.58, p=0.125, BF_{10}=0.587, d=-0.56, Fig 2I). For the cluster analysis, we did two analyses, comparing the Control group data from the single aftereffect block (cycles 291-300) to the Test group data from the first aftereffect block (cycles 121-130) and the second aftereffect block (cycles 291-300). There were no significant clusters when the Test group data came from the first aftereffect block. In contrast, multiple time points in the cluster analysis showed an attenuation effect when the Test group data came from the second aftereffect block (Figs. 2J). These results indicate that the attenuation of implicit adaptation takes place specifically upon relearning and is not attributable to fatigue or habituation.

Discussion

Savings is a relatively ubiquitous phenomenon, observed in domains as diverse as classical conditioning (Kehoe and Macrae, 1997), procedural learning (Crossley et al., 2014), and associative memory (Srull, 1981). Within the domain of sensorimotor learning, savings has been observed in adaptation studies involving perturbations of arm movements (Arce et al., 2010; Krakauer et al., 2005), locomotion (Malone et al., 2011), and saccadic eye movements (Kojima et al., 2004). Recent work has taken a more mechanistic approach, seeking to specify constraints on savings. One key insight here is that the benefits observed during relearning may be limited to certain component processes of learning; in particular, savings has been associated with explicit strategy use, but not implicit sensorimotor adaptation (Haith et al., 2015; Morehead et al., 2015;

see also, Oh and Schweighofer, 2019). Our results go beyond this observation, indicating that implicit adaption not only fails to exhibit savings, but is actually attenuated upon relearning. Taken together, relearning a visuomotor transformation appears to produce opposite effects on explicit strategies and implicit adaptation: While the explicit system exhibits savings, the implicit system shows attenuation.

Attenuation of implicit adaptation upon relearning is a robust phenomenon

The finding that implicit adaptation becomes attenuated upon relearning stands in contrast to prior reports that have either reported an absence of savings (i.e., no change upon relearning, e.g., Morehead et al., 2015) or signatures of savings (e.g., Yin and Wei, 2020). An absence of savings has been interpreted as reflective of the inflexible nature of the implicit adaptation system (Avraham et al., 2019; Bond and Taylor, 2015; Kim et al., 2018; Morehead et al., 2017), consistent with other findings showing that adaptation is minimally influenced by top-down factors such as task outcome (Mazzoni and Krakauer, 2006). By contrast, evidence showing savings during adaptation motivated a model in which the system retains a memory of previously experienced errors, and exhibits increased sensitivity to those errors when re-encountered (Herzfeld et al., 2014). This model can explain behavioral changes in the rate of learning to errors of different size (Marko et al., 2012), as well as manipulations of the learning context (Gonzalez Castro et al., 2014; Herzfeld et al., 2014). However, these behavioral effects may not reflect the memory of errors per se, but rather, the contribution of explicit learning processes that, through the recognition of a particular learning context, recall context-specific strategies that compensate for an associated perturbation (Avraham et al., 2019; Bond and Taylor, 2015; Morehead et al., 2015).

Prior to initiating this project, we were not aware of any reports of attenuation in implicit adaptation during relearning. In retrospect, this may reflect a bias in the literature to look for savings given

the ubiquity of this phenomenon in the learning literature. Moreover, as noted in our motivation for Experiment 2, it can be difficult to obtain “pure” measures of implicit learning. Learning in standard adaptation tasks tends to reflect the composite operation of multiple processes, and it is just in the past decade that analytic methods have been developed to cleanly partition the learning benefits into its component sources (e.g., Benson et al., 2011; Haith et al., 2015; Leow et al., 2018; Schween et al., 2020; Taylor et al., 2014).

Given the unexpected, yet consistent, pattern of attenuation observed in the experiments reported here, we conducted a review of the literature, seeking to determine if this phenomenon had been overlooked in previous studies. Our primary inclusion criteria were 1) that the design included two learning phases with some form of washout between the two phases, and 2) the learning data of interest were estimates of implicit adaption with limited explicit contribution. We note that in most of these studies, the analysis relevant to our review was either not reported or was only noted in passing since the focus was on a different question.

We identified 13 experiments from nine papers that met these inclusion criteria. For each experiment, we calculated the change in performance in re-learning, using Cohen’s *d* as a standardized metric of effect size to facilitate comparison across experiments. In some studies, it was possible to make (or obtain) this calculation from the published work; in the other instances, we obtained the data from the authors, performed the requisite analyses, and then calculated Cohen’s *d*. Consistent with the current results, the overall pattern in these experiments was one of attenuation of implicit adaptation upon relearning, and in the majority of the cases, the effect size was moderate or higher (Fig 3A). The attenuation effect was most pronounced when the experiments included a test for late learning or had an aftereffect block; the results for early learning were inconsistent. We suspect the inconsistency in the early learning results arises in part, from the fact that the level of learning is generally low during this phase, making it less

sensitive for revealing changes between blocks. Moreover, any failure to completely wash out the effects of adaptation from the first block will introduce a bias towards savings.

To detail a few examples, consider first a recent study by Yin and Wei (Yin and Wei, 2020). The focus of the paper was on a generalization issue, showing that following exposure to conditions conducive to implicit adaptation in an initial learning block (e.g., clamped feedback), participants learned at a faster rate when presented with an abrupt 30° (relative to a group who did not receive the initial training). While the behavior here could be seen as a form of savings, it is not clear that the savings came from a change in the implicit process. First, the introduction of the 30° rotation in the second block engages both explicit and implicit processes. Second, veridical feedback was used to washout learning at the end of the first block. This introduces a salient error at the start of washout which might impact subsequent behavior in the second learning block. More relevant to the present discussion is the performance of their control group (Yin and Wei, 2020, Exp 2). For this group, the same 30° rotation was presented in two blocks separated by a washout period (i.e., a classic savings design). Importantly, participants reported their aiming location prior to each reach, and thus, implicit adaptation could be inferred by subtracting the aiming location from the actual hand position (Taylor et al., 2014). As shown in Figure 3B, the estimate of the implicit component was attenuated in the second learning block. A similar pattern was observed in two other studies using the aiming report task (Morehead et al., 2015; Wilterson and Taylor, 2020).

A second example comes from a paper by Leow et al. (Leow et al., 2020). Here the authors used a task in which the target was displaced during the reach such that it intersected the perturbed cursor. This elimination of task error (the cursor “hits” the target) has been argued to provide another method for isolating implicit learning (Leow et al., 2018). When this task was repeated over two blocks, separated by a washout period, the asymptotic level of adaptation was attenuated in the second block (Fig. 3C).

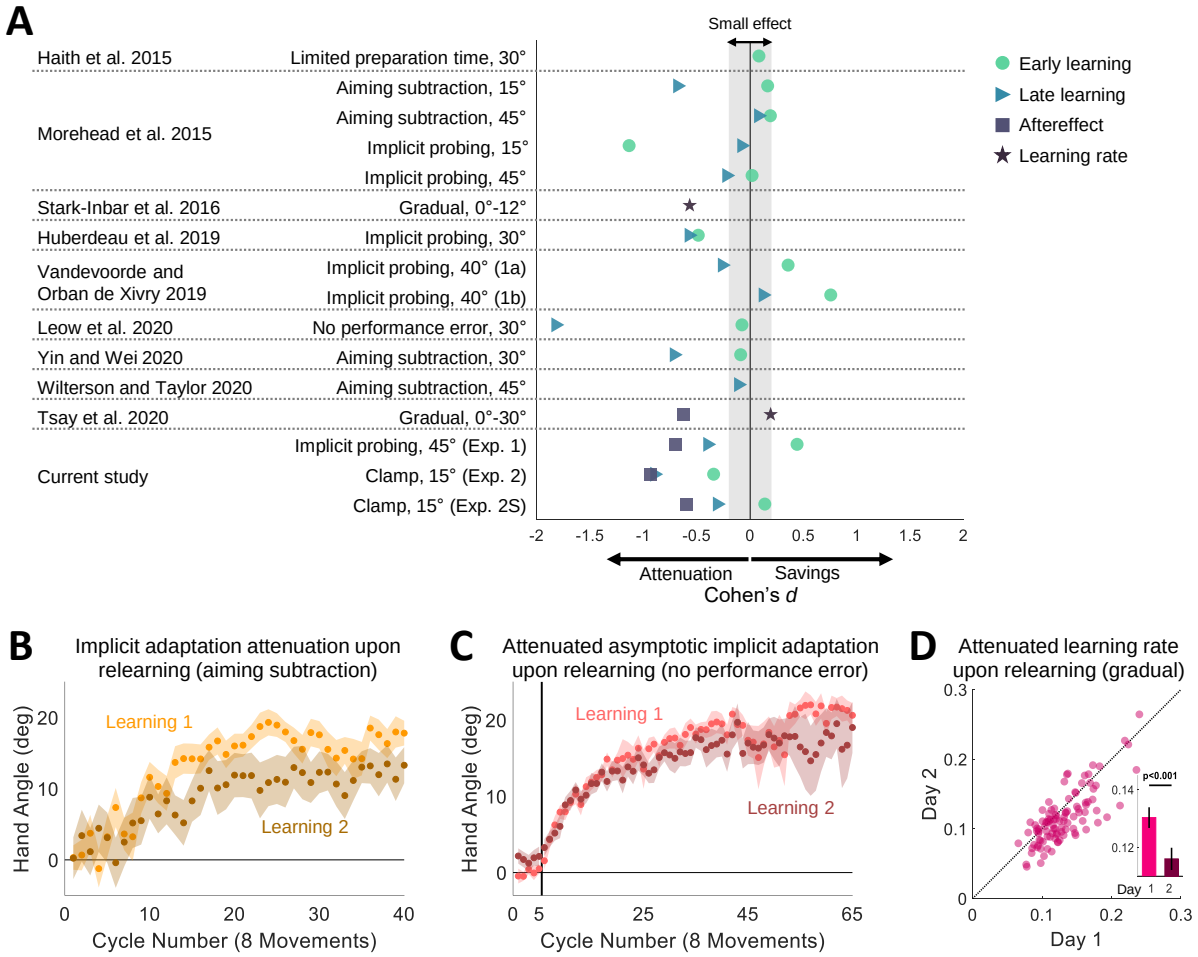


Figure 3. Prior evidence for attenuation upon relearning for implicit visuomotor adaptation.

(**A**) Cohen's *d* effect size of the differences in learning measures between the second and first learning blocks for experiments meeting our criterion for inclusion in the review of the literature. Early learning (green circles), Late learning (blue triangles), Aftereffect (purple squares) and Learning rate (dark purple stars). (**B, C**) Overlaid hand angle functions of implicit adaptation to a visuomotor rotation over two learning blocks separated by a washout phase (not shown). Light and dark colors denote blocks 1 and 2 of the experiment, respectively. Shaded margins represent the SEM. In **B**, implicit adaptation was extracted by subtracting a reported aiming location from movement hand angle on every trial. Adapted with permission from Yin and Wei, 2020. In **C**, implicit adaptive response to the rotated cursor when the target jumps in a manner that eliminates task error. Adapted with permission from Leow et al., 2020. (**D**) Learning rate during adaptation to a gradually changing visuomotor rotation, tested on two days. Pink markers represent individual

participants. Black diagonal dotted line represents the unity line. Bars and black vertical lines (inset) represent mean and SEM, respectively. Adapted with permission from Stark-Inbar et al., 2016.

The third example comes from our own lab, an individual difference study in which participants were tested on a variety of implicit learning tasks, each repeated over two sessions (Stark-Inbar et al., 2016). The battery included a visuomotor rotation task that used a schedule in which the perturbation changed in a gradual manner to minimize awareness. The estimated mean learning rate of the participants was lower on the second day (Fig. 3D). Attenuation was also observed in another study from the lab using a gradual perturbation schedule (Jonathan S. Tsay et al., 2020c).

Our re-analysis of the literature also identified experiments that either showed no significant change in implicit adaptation upon relearning or even savings (see Fig 3A). Notably, all of the cases showing a moderate effect size in the direction of savings used the design of Experiment 1, where participants alternate between Rotation and Probe trials (Morehead et al., 2015, Exp. 4, Vandevoorde and Orban de Xivry, 2019, Exps. 1a and 1b). As noted previously, this method may be problematic for isolating implicit learning due to contamination on Probe trials if the participant fails to dispense with the aiming strategy on some trials. This issue would be most salient in the early stages of learning when differences between strategy use are especially large between the two learning blocks. Indeed, the “savings” effect was mainly found during early learning in these experiments.

We do not take the current results to be indicative of constraints on relearning for all forms of implicit learning. Savings-like phenomena have been observed on implicit tasks involving *de novo* learning, as in mirror drawing and eyeblink conditioning, or when recalibrating an existing representation, as in saccade adaptation. In one of the most widely cited examples, the learning function on a mirror drawing task for the amnesia patient H.M. resumed each day around the same level as where it had ended on the previous session, despite his lack of awareness of having

done the task before (Milner, 1962). While there was no “wash-out” phase to provide a real test of savings, there was no indication that the rate of learning weakened over sessions. Savings has also been well documented in the eyeblink conditioning literature (Macrae and Kehoe, 1999; Medina et al., 2001; Napier et al., 1992; Steinmetz and Freeman, 2014; Woodruff-Pak, 1993) and in saccade adaptation (Kojima et al., 2004).

Possible mechanisms for attenuation upon relearning

We consider two general explanations for an attenuation of relearning rate. First, we discuss how attenuation could come about from the modulation of parameters governing the alteration of a single memory by the error experienced on each movement. We then turn to a hypothesis by which attenuation reflects the interplay of multiple memories. Given that implicit sensorimotor adaptation is paradigmatic as a cerebellar-dependent process (Criscimagna-Hemminger et al., 2010; Izawa et al., 2012; Martin et al., 1996; Morehead et al., 2017; Schlerf et al., 2012; Taylor et al., 2010; Tseng et al., 2007; Weiner et al., 1983), we make reference to other cerebellar-associated learning phenomena in our discussion of these mechanistic hypotheses.

Within the context of sensorimotor adaptation, savings has traditionally been modeled in terms of changes that impact a unitary memory of a sensorimotor map. The classic example is the single rate state-space model (Raibert, 1978; Thoroughman and Shadmehr, 2000). Here, trial-by-trial learning reflects the operation of two parameters, a retention factor corresponding to how well the system retains a memory of its current state, and a learning rate corresponding to how that state should be modified given the error just experienced. With this model, savings can be explained by an increase in retention (Joiner and Smith, 2008) and/or an increase in the learning rate (Herzfeld et al., 2014; Zarahn et al., 2008) across learning blocks. Similarly, eyeblink conditioning is typically modeled with the Rescorla-Wagner model, which formalizes the trial-by-trial change in

the associative strength between the conditioned and unconditioned stimuli in terms of a learning rate parameter and the salience of the CS. Thus, savings could arise from the faster operation of the associative process, or could be attentional in nature, with the salience of the CS amplified when re-encountered in a familiar context (Mackintosh, 1975; Pearce, 2013).

The same models that adjust parameters of a state update equation over experience can account for attenuation in re-learning; in the state-space model, attenuation would result if the retention factor or learning rate were reduced. Indeed, a number of factors that attenuate learning have been modeled this way, including the effect of visual feedback uncertainty (Burge et al., 2008; Jonathan S. Tsay et al., 2020b; Wei and Körding, 2009) and task success (Kim et al., 2019; Leow et al., 2018; Reichenthal et al., 2016).

As shown in the current study, implicit adaptation may be attenuated merely by re-exposure to a perturbation. A simple experience-dependent reduction in either the learning rate or retention parameters is ruled out because the Control group in Experiment 2 showed no attenuation in the magnitude of their asymptotic learning. However, attenuated adaptation upon relearning, as observed in the Test group, could reflect a desensitization process, one in which the system becomes less sensitive to a familiar error when, after washout, that error is re-encountered. Mechanistically, desensitization in re-adaptation of the vestibulo-ocular reflex has been attributed to the saturation of recently activated synapses (Nguyen-Vu et al., 2017). Applying this idea to our results, we might suppose that mechanisms underlying adaptation become saturated during the initial learning block. As long as the environment does not change (as in the Control group), the system can remain at asymptote. However, desensitization would occur during re-learning if the washout phase did not allow sufficient time to rejuvenate synaptic elements required for plasticity. This hypothesis predicts that the degree of attenuation would be dependent on the duration of the washout phase: Less attenuation should be seen if the duration of the washout phase is increased. However, the fact that attenuation of implicit adaptation is observed across

days (Stark-Inbar et al., 2016; Jonathan S. Tsay et al., 2020c; Wilterson and Taylor, 2020) seems problematic for this unitary memory hypothesis.

An alternative framework for understanding attenuation during re-learning is to consider how learning functions may be modulated by the interplay of multiple memories. Various reformulations of the state-space model have been developed to incorporate this idea. For example, the basic state-space model can be expanded to allow for multiple learning processes that operate on different time scales (Smith et al., 2006; see also Kording et al., 2007). Interestingly, the interplay of fast and slow processes, even when their associated parameters remain fixed, can produce savings, at least when the washout period is not sufficiently long to allow both processes to return to the null state (Zarahn et al., 2008).

In a complementary way, attenuation in re-learning may also reflect the interplay of component processes that have opposing effects on behavior. In studies of sensorimotor adaptation, interference is observed when opposing perturbations alternate in a random manner (Howard et al., 2013), as well as when presented sequentially (Miall et al., 2004; Shadmehr and Brashers-Krug, 1997). In such situations, the absence of savings has been attributed to interference between two internal models, one associated with each perturbation (Krakauer et al., 2005). Similarly, savings is abolished in saccade adaptation with a protracted washout period (Kojima et al., 2004), as well as in conditioning studies when the extinction phase involves the repeated presentation of the CS and US in an unpaired manner (Bouton et al., 2004; Frey and Butler, 1977). Theoretically, in these manipulations, a reversed perturbation or decoupling of the CS-US relationship leads to the establishment of a new memory, one that produces interference when the original situation is re-encountered (Haruno et al., 2001; Jordan and Jacobs, 1994).

Interference can, of course, not only abolish savings, but also produce attenuation in relearning when the irrelevant memory trace continues to contribute to performance. This idea has been extensively examined in the classical conditioning literature. For example, in fear conditioning,

attenuation is observed when there is an extended extinction period involving just the presentation of the CS alone (e.g., tone that had been associated with a foot shock) (Bouton, 1986). The reduced rate of learning observed when the CS is again paired with the US has been modeled as resulting from competition between two memories, one reflecting the paired CS-US association leading to a CR, and the other the solitary CS, associated with no response. This model nicely accounts for the fact that attenuation is especially pronounced when the extinction period is long and when the context remains unchanged (Bouton, 2002; Bouton and Swartzentruber, 1989).

It remains to be seen if similar constraints are relevant to the attenuation observed in the current study. Given concerns with residual effects from the first adaptation block, we designed the studies to ensure a strong washout phase: We used a large number of veridical feedback trials in Experiment 1 and a reversed clamp, followed by veridical feedback in Experiments 2 and 2S. These manipulations would be conducive sources of interference (e.g., extended association with veridical feedback in the experimental context). We note that the multi-session study of Wilterson and Taylor (Wilterson and Taylor, 2020) did not include a washout phase, and the interference hypothesis would not seem a viable explanation for the modest attenuation observed across sessions (see Fig. 3A). However, interference here may be between the laboratory and natural motor behavior that occurs once the participant has left the lab between sessions.

To this point, we have elaborated on two general models of how learning might be modulated as a function of experience: Changes in the parameters of a single memory, or an interplay between different learning processes, each having a specific set of stable parameters. A hybrid of these two approaches has been offered to explain savings in situations where neither approach is sufficient on its own (Mawase et al., 2014; Zarahn et al., 2008). For example, in an extension of the multi-rate idea, Hadjiosif and Smith (Hadjiosif and Smith, 2013) proposed that savings was restricted to the fast, labile process, with the rate of learning for this process increased upon re-exposure to a perturbation.

The distinction we observed between explicit and implicit learning processes in terms of savings can also be understood from this hybrid perspective. It seems clear that explicit processes such as aiming can, and do, exhibit savings (Haith et al., 2015; Leow et al., 2020; Morehead et al., 2015). While this could be modeled by postulating a faster learning rate or stronger retention rate, the underlying psychological process is likely one of memory retrieval. When re-exposed to a perturbation in a familiar context, the participant recalls a successful strategy (Morehead et al., 2015). Using methods that allowed us to isolate the contribution of implicit processes revealed the opposite behavioral profile here, one of attenuation during relearning. Determining if this attenuation arises from a desensitization of an implicit process (or processes), or interference from the implicit interplay of multiple memories remains a question for future study.

Methods

Ethics Statement

The study was approved by the Institutional Review Board at the University of California, Berkeley. All participants provided written informed consent to participate in the study.

Participants

104 healthy volunteers (aged 18-40 years; 64 females) were tested, 24 in Experiment 1, 32 in Experiment 2, and 48 in Experiment 2S. In Experiments 1 and 2, all participants were right-handed, as verified with the Edinburgh Handedness Inventory (Oldfield, 1971). The participants in Experiment 2S did not complete a handedness inventory, but 42 of them self-reported being right-handed, 4 left-handed and 2 ambidextrous. The sample size for each experiment was set to include ~30% more participants than the minimum required to ensure good statistical power, and appropriate counter-balancing of the perturbation direction and target location sets (details provided in the protocol for each experiment).

Experimental setup and task

The participant sat at a custom-made table that housed a horizontally mounted LCD screen (53.2 cm by 30 cm, ASUS), positioned 27 cm above a digitizing tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA). Stimuli were displayed on the LCD screen. The experimental software was custom written in Matlab [The MathWorks, Natick, MA], using the Psychtoolbox extensions (Brainard, 1997).

The participant performed center-out movements by sliding a modified air hockey paddle containing an embedded digitizing stylus across the tablet. The tablet recorded the position of the stylus at 200 Hz. The monitor occluded direct vision of the hand, and the room lights were extinguished to minimize peripheral vision of the arm.

At the beginning of each trial, a white circle (0.5 cm diameter) appeared on the center of the screen, indicating the start location. The participant moved her hand (holding the stylus) to the start location. Feedback of hand position was indicated by a white cursor (0.3 cm diameter), and only provided when the hand was within 1 cm of the start location. There was a ~33 ms delay between the sampling of the tablet and update of the cursor position based on that sample. After the hand position was maintained in the start location for 500 ms, a colored target (0.5 cm diameter circle) appeared at one of four locations around a virtual circle, with a radial distance of 8 cm from the start location. Within each experimental group, the target locations were in a diagonal layout, at 45° (0° being the positive edge of the abscissa), 135°, 225°, 335° for half of the participants and in an oblique layout, at 20°, 110°, 200°, 290° for the other half of the participants.

The participant was instructed to rapidly move her hand following the presentation of the target, attempting to slice through the target with either the hand or cursor (depending on the specific experimental protocol). Movement time was calculated as the interval between the time at which

the amplitude of the movement exceeded 1 cm from the start location to the time at which the amplitude reached a radial distance of 8 cm, the target distance. To encourage the participants to move fast, the auditory message “too slow” was played if the movement time exceeded 300 ms. Participants had little difficulty meeting this criterion, with an overall mean movement time across the two experiments of 132±4.16 (± standard error of the mean, SEM). After moving to the target, the participant moved back to the start location. The overall mean time required to return to the start position was 1.69±0.05 s.

Experimental protocol

The primary goal of the study was to evaluate changes in implicit adaptation upon relearning. Thus, the general design in each experiment incorporated two learning blocks that were separated by a long washout block.

Experiment 1

24 participants were tested in Experiment 1. The target number of participants was determined based on the effect size (d=0.67) observed for savings in a previous study that used a similar protocol (Morehead et al., 2015), with a significance level of α=0.05 and power of 0.8. This analysis yielded a minimum sample size of 16 participants. The tested number was increased given a criterion to increase the sample size by at least 30% above the minimum and counter-balancing considerations.

The experimental session consisted of 180 movement cycles, each involving four movements, one to each target. As mentioned above, the targets were positioned either in a diagonal or oblique layout. A diagonal layout is commonly used in visuomotor rotation studies (e.g., Krakauer et al., 2000; Taylor et al., 2014). However, we were concerned that a 4-target diagonal layout might be conducive for finding an optimal aiming solution to counteract a 45° rotation (see below)

since these would require movements along the cardinal directions (in the absence of implicit adaptation). For this reason, we opted to use an oblique layout for half of the participants.

The session was divided into the following blocks (Fig. 1B): No Feedback Baseline (10 cycles), Veridical Feedback Baseline (10 cycles), Learning 1 (50 cycles), Aftereffect 1 (10 cycles), Washout (40 cycles), Learning 2 (50 cycles) and Aftereffect 2 (10 cycles). The initial baseline blocks were included to familiarize the participants with the experimental setup. In these trials, participants were instructed to move their hand directly to a blue target. Veridical feedback was provided in the second baseline block to minimize idiosyncratic reaching biases.

Two types of trials were randomly interleaved during the learning blocks: Rotation and Probe trials. For the Rotation trials (40 cycles per block), the position of the cursor was rotated by 45° with respect to the position of the hand. We chose a rotation size of 45° because adaptation to a perturbation of this size reliably produces savings upon relearning (Morehead et al., 2015; Zarahn et al., 2008). The direction of the rotation (clockwise or counterclockwise) was fixed for a given participant and counterbalanced across participants. On Rotation trials, the color of the target was red, providing a cue that the cursor position would be perturbed. At the start of the block, the participant was instructed that a red target signified that the cursor “will act differently”, and that their goal was to make the cursor hit the target.

For the Probe trials (10 cycles per block), the color of the target was blue. The participant was instructed that the cursor would not be visible on these trials and that their goal was different: Now they were to reach directly to the blue target, discontinuing any strategy they might have adopted when reaching to the red targets. To emphasize these instructions, the message “Move your hand to the target” appeared simultaneously with the blue target. The position of the instruction was either above or below the center of the screen, selected on each trial to be closest to the target (above for targets between 0°-180° and below for targets between 180°-360°).

To minimize possible effects related to switching between the two types of trials, the participants were informed that, while they could initiate the reach at any time after the onset of the target, they should take their time to comply with the instructions/goal associated with each target color. After cycles 40 and 130, the midpoints of the learning blocks, the participant was provided with a 1-minute break.

To provide another measure of implicit adaptation, following each of the learning blocks, we included aftereffect blocks (1 and 2) in which the feedback was eliminated in all trials. Just before the start of the aftereffect block, the participant was informed that the cursor would no longer be visible and that the task was to move her hand directly to the target. There was no additional break prior to the start of the aftereffect block, minimizing the time for learning to decay.

The washout block was introduced following the first aftereffect block and a 2-minute rest period. During this block, the participant was instructed to reach directly to the target and veridical feedback was provided on each trial with the aim of bringing the sensorimotor map back to a baseline state. The minimal number of washout cycles (40) was set to be the same number as that used during the learning block and should be sufficient to ensure full unlearning (Morehead et al., 2015). We included three 1-minute breaks during the block to verify that the effects of implicit adaptation were completely washed out by the beginning of the second learning block. These probes have been shown to be useful in revealing residual effects of adaptation, manifest as transient increases in hand angle after the break (Vandevoorde and Orban de Xivry, 2019).

<u>Experiment 2</u>

Participants in Experiment 2 were assigned to either the Test (N=16) or Control (N=16) condition. The target number of participants was determined based on the effect size (d=0.70) of the attenuation effect observed in the aftereffect data in Experiment 1. This analysis yielded a minimum sample size of 12 participants, with the actual number tested based on the criterion to

increase the sample size by at least 30% above the minimum and counter-balancing considerations.

The experimental session consisted of 300 movement cycles of four movements (to four target locations, see above). For the Test group, the session was divided into the following blocks (Fig. 2B): No Feedback Baseline (10 cycles), Veridical Feedback Baseline (10 cycles), Clamp 1 (100 cycles), Aftereffect 1 (10 cycles), Washout (60 cycles), Clamp 2 (100 cycles), and Aftereffect 2 (10 cycles).

To isolate implicit adaptation, we used task-irrelevant clamped feedback in the Clamp blocks. Here the cursor moved in a fixed path, displaced 15° from the target (clockwise or counterclockwise, fixed for each participant and counterbalanced). The radial position of the feedback cursor corresponded to the participant's hand, but the angular position of the cursor was invariant, independent of the participant's reaching direction. The participant was instructed to ignore the feedback and always reach directly to the target. To make this salient, two demonstration trials were performed prior to each clamp block. On each demonstration trial, the target appeared at the 78° location. For the first trial, the participant was told to "Reach straight to the left" (180°); for the second trial, the participant was told to "Reach backwards towards your body" (270°). On both trials, the cursor trajectory was clamped, following the same 15° path off from the target that the participant would experience throughout the Clamp blocks. The clamped feedback offset of 15° falls within the range of error sizes that induce an invariant rate and magnitude of adaptation (~6°- 60°, Kim et al., 2018).

Aftereffect blocks with no feedback were introduced immediately following each of the Clamp blocks. The participant was informed before each block that the cursor would not be visible and was instructed again to move directly to the target.

Rather than using veridical feedback in the washout block (as in Experiment 1), we adopted a different procedure to eliminate the effects of adaptation in Experiment 2. The introduction of veridical feedback after the conclusion of the first clamp block would result in a relatively large discrepancy between the expected and observed feedback, assuming adaption has occurred. We were concerned that this would make participants aware of the change in behavior, and that this might alter their response to the clamped feedback in the second clamp block (e.g., invoke a strategy to offset the anticipated effects of adaptation). To minimize awareness of adaptation, the washout block consisted of two phases. In the first phase, we reversed the direction of the clamp. The participant was informed that she would again not have control over the movement direction of the feedback, and reminded to ignore the feedback, aiming directly for the target. This manipulation induced a reversal in adaptation, and thus drove the direction of the hand back towards the target. When the median reach direction was within 5° of the target for six consecutive cycles, the second phase was implemented. Here the feedback became veridical. Given that the total number of washout cycles was fixed, the number of cycles in each phase was determined on an individual basis using the performance criterion described above. All of the participants in the Test group experienced at least 30 cycles (37.3±1.62) of veridical feedback before the second clamp block, ensuring they had sufficient exposure to unperturbed feedback prior to the onset of the second learning block. Demonstration trials were provided at the start of each phase of the washout block, two for the reversed clamp and two for veridical feedback. The demonstration trials were similar to those presented before the clamp blocks (same target location and same instructions for where to reach). The provided feedback was matched to feedback in the subsequent phase (reversed clamp/veridical). Note that the demonstration trials for the veridical feedback phase appeared in the transition between the phases, when the participant already reached close to the targets.

The Control group was included to provide a between-group comparison to the performance of the Test group during the second clamp block. For the Control group, the session was divided into the following blocks (Fig. 2B): No Feedback Baseline (10 cycles), Veridical Feedback Baseline (10 cycles), extended Clamp (270 cycles), and No Feedback Aftereffect (10 cycles). The two demonstration trials were presented at the start of the clamp block.

Breaks were included throughout the experiment similar to those included in Experiment 1. They were provided for both groups at the following stages corresponding to the experimental protocol of the Test group: the middle of each clamp block (after cycles 70 and 240, 1 min), just before the start of the washout block (cycle 130, 2 min), and at three time points (1 min) in the washout block (cycles 167, 174 and 181).

At the end of experiment, participants completed a short survey. To verify that the participants understood the task and followed the instructions, we asked: “Did you ever try to reach your hand to places other than the target?” To evaluate the awareness of the participants about the change in behavior, we asked: “Do you think you changed your behavior at all during the experiment?”

Experiment 2S

Experiment 2S was conducted to provide a replication test of the results obtained with the Test group in Experiment 2. We used an online platform created within the lab for conducting sensorimotor learning studies (Jonathan S. Tsay et al., 2020a). Participants (N=48) were recruited using the crowdsourcing website Prolific (www.prolific.co). Since participants performed the experiment remotely with their personal computer, the test apparatus varied across participants. Based on self-report data, 29 participants used an optical mouse and 19 used a trackpad. Monitor sizes varied between 11-27 inches. Based on power calculations from the aftereffect data in Experiment 2, a minimum sample size of 9 would be required (d=0.94). However, given the results

from pilot work indicating that online data would be more variable and show a lower asymptotic level of adaptation, we opted to use a large sample size.

The experimental design was similar to that used for the Test group in Experiment 2 with a few minor modifications. First, the two Clamp blocks consisted of 80 cycles each, and the washout block (individually determined combination of reversed-clamp and veridical feedback trials) was extended to a total of 80 cycles. Second, we did not program in any breaks.

Data analysis

The kinematic data recorded from the digitizing tablet were analyzed offline using custom-written MATLAB code. The primary dependent variable was the direction of hand movement (hand angle). For each trial, we identified the position of the hand-held stylus when the movement amplitude was equal or larger than the radial distance to the target (8 cm). Hand angle was defined as the angle formed by a line connecting this point with the movement origin (the center of the start location), and a line connecting the target position with the movement origin. For participants who experienced a counterclockwise perturbation (rotation or clamp), the sign of the hand angle was flipped. In this manner, a positive hand angle indicates movement in the opposite direction of the perturbed feedback, the expected change due to adaptation. The mean hand angle for each movement cycle was calculated by averaging the hand angle of four consecutive reaches (one reach to each of the four different target locations).

In all three experiments (Exps. 1, 2, and 2S), we observed no reliable differences on the measures of relearning between sub-groups experiencing a clockwise or counter-clockwise rotation and between sub-groups reaching to targets positioned along the diagonal layout or oblique layout. As such, we collapsed the data across the sub-groups.

For Experiments 1 and 2, all trials were included in the analysis (with one exception, noted below). We opted to not take any steps to exclude outliers given that participants in Experiment 1

frequently exhibit high levels of exploration after experiencing a large perturbation when instructed to focus on making the cursor hit the target. As such, we anticipated that there would be large trial-by-trial variability during the Rotation trials, at least in the first learning block, making it difficult to define, a priori, criteria for outlier removal. For consistency, we opted to also use all of the data in Experiment 2, although participants do not exhibit exploratory behavior in response to clamped feedback. We note that none of the statistical analyses were changed if repeated after exclusion of outliers (0.6% of all trials). Due to the randomization algorithm in the presentation of the Probe trials in Experiment 1, the first trial in the first (but not the second) learning block was a Probe trial. Since it was presented before any Rotation trials, the data from this trial were not included in the analysis.

We applied an outlier removal algorithm in Experiment 2S since a preliminary review of the data indicating some large deviations from the target, likely indicative of lapses of attention during the extended unsupervised testing session. We excluded trials in which the hand angle deviated from the target location by more than 100° and trials in which the absolute trial-to-trial change in hand angle was larger than 20°. Based on these criteria, a total of 1.8% of all trials were excluded.

The following measures of learning were calculated: Early learning, Late learning and Aftereffect. Separate measures were calculated for the Rotation and Probe data in each learning block of Experiment 1, and for the data in each of the two clamp blocks of Experiment 2 (only one block for the Control group). For Rotation trials in Experiment 1 and Clamp trials in Experiment 2, Early learning and Late learning were defined as the mean hand angle over cycles 3–7 and the last ten cycles of each learning block, respectively (Figs. 1B, 2C). Note that in Experiment 1, there is one cycle of Probe trials for every four cycles of Rotations trials. Thus, to examine learning within similar time windows for the Rotation and Probe trials, Early learning for the Probe trials was based on cycles 1-2 and Late learning was based on the last two cycles (cycles 9-10) in each

learning block. Aftereffect was defined as the mean hand angle over the first cycle of the no-feedback aftereffect block.

Movement time was calculated as the interval between the time at which the amplitude of the movement exceeded 1 cm from the start location to the time at which the amplitude reached the radial distance of the target. Although not emphasized in the instructions, reaction time was calculated as the interval between the appearance of the target and the time that the hand position exceeded a distance of 1 cm from the start location. Total trial time was calculated as the sum of reaction time, movement time and inter-trial interval, measured as the time required to move back to the start location. For each participant, we calculated the median of each measure over all trials in a given cycle (for trial time analysis), a given learning condition/block (for reaction time analysis), or over all the trials in the experiment (for analysis of movement time).

Statistical analysis

Two statistical approaches were used to analyze the changes in hand angle that occurred in response to the feedback perturbations. The first was based on an approach frequently adopted in the sensorimotor adaptation literature (e.g., Leow et al., 2012; Taylor et al., 2014; Wong et al., 2019), focusing on pre-defined cycles to examine different phases of learning (early, late, aftereffect). To examine changes in behavior within each of the two learnings blocks and between the two blocks, we used a two-way repeated measures ANOVA, with two within-participant factors, Stage (Early and Late) and Block (Learning 1 and Learning 2). Given our focus on the between block changes (e.g., savings), we included planned comparisons, using paired-sample *t* tests to analyze the changes between blocks 1 and 2. We also used an independent two-sample, between-participant *t* test to compare the Control and Test groups. Two-tailed *t* tests were used in all of these analyses, with the statistical significance threshold set at the $p<0.05$. For all of the *t* tests, we report the Bayes factor BF_{10}, the ratio of the likelihood of the alternative hypothesis (H_1) over the null hypothesis (H_0) (Kass and Raftery, 1995) and the Cohen's *d* effect size (Cohen,

2013). For the repeated-measures ANOVA, the effect size is reported using partial eta-squared (η_p^2). All of the measurements met the assumption of normality based on the Lilliefors test (Lilliefors, 1967).

Although defined *a priori* based on previous studies, specifying a subset of the cycles as of principle interest is somewhat arbitrary, and ignores much of the data. The second statistical approach was chosen to avoid these concerns. Here we opted to use a nonparametric permutation test (Maris and Oostenveld, 2007) that is widely employed in the analysis of multivariate data in which there are autocorrelations between sequential data points (e.g., as with EEG data, see Arnal et al., 2015; Fell et al., 2011). This “cluster analysis” approach seems well-suited for the continuous and autocorrelated nature of the data obtained in studies of sensorimotor adaptation. We used this test to identify clusters of cycles in which the hand angle differed between the two Learning blocks and Aftereffect blocks. Two-tailed paired-sample *t* tests were performed for each cycle within the blocks of interest. We then defined consecutive cycles in which the difference was significant ($p<0.05$) as a ‘cluster’, and calculated for each cluster, the sum of the t-values that were obtained for the cycles in that cluster (referred to as a t-sum statistic). A null distribution of the t-sum statistic was constructed by performing 10,000 random permutations with the data: For each permutation, the data for a given participant was randomly assigned to “block 1” or “block 2”. For each permuted data set, we performed the same cluster-identification procedure as was done with the actual data and calculated the t-sum statistic for each cluster. In cases where several clusters were found for a given null set permutation, we recorded the t-sum statistic of the cluster with the largest t-sum value. Thus, the generated null distribution is composed of the maximal t-sum values achieved by chance, a method that controls for the multiple comparisons involved in this analysis (Maris and Oostenveld, 2007). Each of the clusters identified in the non-permuted data were considered statistically significant only if its t-sum was larger than 95% of the t-sums in the null distribution, corresponding to a p-value of 0.05.

In Experiment 2, a between-subject cluster analysis was used to compare, in separate analyses, the aftereffect data from the Control group with the aftereffect data obtained from the Test group after Clamp 1 or Clamp 2 (using independent two-sample *t* tests).

To examine within-participant changes in reaction time between the two learning blocks, paired-sample *t* tests were used.

Effect size analysis of prior studies

For the review of previous work, we identified nine papers that included conditions to provide a test of the attenuation phenomenon. Some reported multiple experiments, bringing the final total to 13 experiments. Although these experiments entail a broad range of methods, we calculated the effect size for the contrast of interest to put the results in a common context. For studies that directly compared adaptation measures between the sessions, we calculated Cohen's *d* from the reported comparisons. For the other studies, we obtained the data from the authors, performed the relevant analysis, and then computed Cohen's *d*.

Based on the design used in these studies, we classified an analysis as either early, late, aftereffect and/or learning rate (see Figure 3) using criteria reported in the study or selected to approximate the manner in which these phases were defined in the present study. The specific criteria were:

'Limited preparation time' paradigm (Haith et al., 2015): Early learning only, comparing the first 5 trials of the perturbation phase relative to the last 5 trials of a baseline phase.

'Aiming subtraction' (Morehead et al., 2015; Wilterson and Taylor, 2020; Yin and Wei, 2020) and 'No performance error' (Leow et al., 2020) paradigms: Early and Late learning, defined as the mean hand angle over trials/cycles 3–7 and the last ten trials or cycles of the of each learning block, respectively.

‘Implicit probing’ paradigm (Morehead et al., 2015; Huberdeau et al., 2019; Vandevoorde and Orban de Xivry, 2019): Early and Late learning, based on the first and last two trials or cycles of each learning block, respectively.

‘Gradual’ paradigm (Stark-Inbar et al., 2016; Jonathan S. Tsay et al., 2020c): Learning rate based on model-based estimate of learning (Thoroughman and Shadmehr, 2000), calculated across the entire block. This measure reflects the proportional trial-by-trial change in hand angle with respect to the experienced error. The Aftereffect (only for Tsay et al.), defined as the mean hand angle over the first cycle of a no-feedback aftereffect block.

Acknowledgments

We thank Maya Malaviya, Sarvenaz Pakzad, Marina Iranmanesh and Utsav Kapoor for their assistance with data collection. We thank Assaf Breska for helpful comments on the manuscript. This work was supported by grants NS116883, NS105839 and DC017091 from the National Institutes of Health (NIH). HEK was funded by grants K12 HD055931 from the NIH and M3X 1934650 from the National Science Foundation.

References

Arce F, Novick I, Mandelblat-Cerf Y, Vaadia E. 2010. Neuronal Correlates of Memory Formation in Motor Cortex after Adaptation to Force Field. *J Neurosci* **30**:9189–9198. doi:10.1523/JNEUROSCI.1603-10.2010

Arnal LH, Doelling KB, Poeppel D. 2015. Delta–Beta Coupled Oscillations Underlie Temporal Prediction Accuracy. *Cereb Cortex* **25**:3077–3085. doi:10.1093/cercor/bhu103

Avraham G, Keizman M, Shmuelof L. 2019. Environmental consistency modulation of error sensitivity during motor adaptation is explicitly controlled. *Journal of Neurophysiology* **123**:57–69. doi:10.1152/jn.00080.2019

Benson BL, Anguera JA, Seidler RD. 2011. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology* **105**:2843–2851. doi:10.1152/jn.00002.2011

Berniker M, Kording KP. 2011. Estimating the Relevance of World Disturbances to Explain Savings, Interference and Long-Term Motor Adaptation Effects. *PLoS Comput Biol* **7**. doi:10.1371/journal.pcbi.1002210

Bond KM, Taylor JA. 2015. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology* **113**:3836–3849. doi:10.1152/jn.00009.2015

Bouton ME. 2002. Context, ambiguity, and unlearning: sources of relapse after behavioral extinction. *Biological Psychiatry* **52**:976–986. doi:10.1016/S0006-3223(02)01546-9

Bouton ME. 1986. Slow reacquisition following the extinction of conditioned suppression. *Learning and Motivation* **17**:1–15. doi:10.1016/0023-9690(86)90017-2

Bouton ME, Swartzentruber D. 1989. Slow reacquisition following extinction: Context, encoding, and retrieval mechanisms. *Journal of Experimental Psychology: Animal Behavior Processes* **15**:43–53. doi:10.1037/0097-7403.15.1.43

Bouton ME, Woods AM, Pineño O. 2004. Occasional reinforced trials during extinction can slow the rate of rapid reacquisition. *Learning and Motivation* **35**:371–390. doi:10.1016/j.lmot.2004.05.001

Brainard DH. 1997. The Psychophysics Toolbox. *Spatial Vision* **10**:433–436. doi:10.1163/156856897X00357

Burge J, Ernst MO, Banks MS. 2008. The statistical determinants of adaptation rate in human reaching. *Journal of Vision* **8**:20–20. doi:10.1167/8.4.20

Cohen J. 2013. Statistical Power Analysis for the Behavioral Sciences. Academic Press.

Coltman SK, Cashaback JGA, Gribble PL. 2019. Both fast and slow learning processes contribute to savings following sensorimotor adaptation. *Journal of Neurophysiology* **121**:1575–1583. doi:10.1152/jn.00794.2018

Criscimagna-Hemminger SE, Bastian AJ, Shadmehr R. 2010. Size of Error Affects Cerebellar Contributions to Motor Learning. *Journal of Neurophysiology* **103**:2275–2284. doi:10.1152/jn.00822.2009

Crossley MJ, Ashby FG, Maddox WT. 2014. Context-dependent savings in procedural category learning. *Brain and Cognition* **92**:1–10. doi:10.1016/j.bandc.2014.09.008

Day KA, Roemmich RT, Taylor JA, Bastian AJ. 2016. Visuomotor Learning Generalizes Around the Intended Movement. *eNeuro* **3**. doi:10.1523/ENEURO.0005-16.2016

Ebbinghaus H. 1913. Memory (ha ruger & ce bussenius, trans.). *New York: Teachers College(Original work published 1885)* **39**.

Fell J, Ludowig E, Staresina BP, Wagner T, Kranz T, Elger CE, Axmacher N. 2011. Medial Temporal Theta/Alpha Power Enhancement Precedes Successful Memory Encoding: Evidence Based on Intracranial EEG. *J Neurosci* **31**:5392–5397. doi:10.1523/JNEUROSCI.3668-10.2011

Frey PW, Butler CS. 1977. Extinction after aversive conditioning: An associative or nonassociative process? *Learning and Motivation* **8**:1–17. doi:10.1016/0023-9690(77)90063-7

Gonzalez Castro LN, Hadjiosif AM, Hemphill MA, Smith MA. 2014. Environmental Consistency Determines the Rate of Motor Adaptation. *Current Biology* **24**:1050–1061. doi:10.1016/j.cub.2014.03.049

Hadjiosif A, Smith MA. 2013. Savings is restricted to the temporally labile component of motor adaptation. *Translational and Computational Motor Control* 409–419.

Hadjiosif AM, Criscimagna-Hemminger SE, Gibo TL, Okamura AM, Shadmehr R, Bastian AJ, Smith MA. 2014. Cerebellar damage reduces the stability of motor memories. *Proceeding of the translational and computational motor control*.

Haith AM, Huberdeau DM, Krakauer JW. 2015. The Influence of Movement Preparation Time on the Expression of Visuomotor Learning and Savings. *J Neurosci* **35**:5109–5117. doi:10.1523/JNEUROSCI.3869-14.2015

Haruno M, Wolpert DM, Kawato M. 2001. MOSAIC Model for Sensorimotor Learning and Control. *Neural Computation* **13**:2201–2220. doi:10.1162/089976601750541778

Herzfeld DJ, Vaswani PA, Marko M, Shadmehr R. 2014. A memory of errors in sensorimotor learning. *Science* 1253138. doi:10.1126/science.1253138

Howard IS, Wolpert DM, Franklin DW. 2013. The effect of contextual cues on the encoding of motor memories. *Journal of Neurophysiology* **109**:2632–2644. doi:10.1152/jn.00773.2012

Huang VS, Haith A, Mazzoni P, Krakauer JW. 2011. Rethinking Motor Learning and Savings in Adaptation Paradigms: Model-Free Memory for Successful Actions Combines with Internal Models. *Neuron* **70**:787–801. doi:10.1016/j.neuron.2011.04.012

Huberdeau DM, Haith AM, Krakauer JW. 2015. Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *Journal of Neurophysiology* **114**:969–977. doi:10.1152/jn.00369.2015

Huberdeau DM, Krakauer JW, Haith AM. 2019. Practice induces a qualitative change in the memory representation for visuomotor learning. *Journal of Neurophysiology* **122**:1050–1059. doi:10.1152/jn.00830.2018

Izawa J, Criscimagna-Hemminger SE, Shadmehr R. 2012. Cerebellar Contributions to Reach Adaptation and Learning Sensory Consequences of Action. *J Neurosci* **32**:4230–4239. doi:10.1523/JNEUROSCI.6353-11.2012

Joiner WM, Smith MA. 2008. Long-Term Retention Explained by a Model of Short-Term Learning in the Adaptive Control of Reaching. *Journal of Neurophysiology* **100**:2948–2955. doi:10.1152/jn.90706.2008

Jordan MI, Jacobs RA. 1994. Hierarchical Mixtures of Experts and the EM Algorithm. *Neural Computation* **6**:181–214. doi:10.1162/neco.1994.6.2.181

Kagerer FA, Contreras-Vidal JL, Stelmach GE. 1997. Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp Brain Res* **115**:557–561. doi:10.1007/PL00005727

Kass RE, Raftery AE. 1995. Bayes Factors. *Journal of the American Statistical Association* **90**:773–795. doi:10.1080/01621459.1995.10476572

Kehoe EJ, Macrae M. 1997. Savings in animal learning: Implications for relapse and maintenance after therapy. *Behavior Therapy* **28**:141–155. doi:10.1016/S0005-7894(97)80039-1

Kim HE, Avraham G, Ivry RB. 2020. The Psychology of Reaching: Action Selection, Movement Implementation, and Sensorimotor Learning. *Annu Rev Psychol*. doi:10.1146/annurev-psych-010419-051053

Kim HE, Morehead JR, Parvin DE, Moazzezi R, Ivry RB. 2018. Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Communications Biology* **1**:19. doi:10.1038/s42003-018-0021-y

Kim HE, Parvin DE, Ivry RB. 2019. The influence of task outcome on implicit motor learning. *eLife* **8**:e39882. doi:10.7554/eLife.39882

Kojima Y, Iwamoto Y, Yoshida K. 2004. Memory of Learning Facilitates Saccadic Adaptation in the Monkey. *J Neurosci* **24**:7531–7539. doi:10.1523/JNEUROSCI.1741-04.2004

Kording KP, Tenenbaum JB, Shadmehr R. 2007. The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience* **10**:779–786. doi:10.1038/nn1901

Krakauer JW, Ghez C, Ghilardi MF. 2005. Adaptation to Visuomotor Transformations: Consolidation, Interference, and Forgetting. *J Neurosci* **25**:473–478. doi:10.1523/JNEUROSCI.4218-04.2005

Krakauer JW, Pine ZM, Ghilardi M-F, Ghez C. 2000. Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *J Neurosci* **20**:8916–8924. doi:10.1523/JNEUROSCI.20-23-08916.2000

Labruna L, Stark-Inbar A, Breska A, Dabit M, Vanderschelden B, Nitsche MA, Ivry RB. 2019. Individual differences in TMS sensitivity influence the efficacy of tDCS in facilitating sensorimotor adaptation. *Brain Stimulation* **12**:992–1000. doi:10.1016/j.brs.2019.03.008

Leow L-A, Loftus AM, Hammond GR. 2012. Impaired savings despite intact initial learning of motor adaptation in Parkinson's disease. *Exp Brain Res* **218**:295–304. doi:10.1007/s00221-012-3060-5

Leow L-A, Marinovic W, Rugy A de, Carroll TJ. 2020. Task Errors Drive Memories That Improve Sensorimotor Adaptation. *J Neurosci* **40**:3075–3088. doi:10.1523/JNEUROSCI.1506-19.2020

Leow L-A, Marinovic W, Rugy A de, Carroll TJ. 2018. Task errors contribute to implicit aftereffects in sensorimotor adaptation. *European Journal of Neuroscience* **48**:3397–3409. doi:10.1111/ejn.14213

Lilliefors HW. 1967. On the Kolmogorov-Smirnov Test for Normality with Mean and Variance Unknown. *Journal of the American Statistical Association* **62**:399–402. doi:10.1080/01621459.1967.10482916

Mackintosh NJ. 1975. A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review* **82**:276–298. doi:10.1037/h0076778

Macrae M, Kehoe EJ. 1999. Savings after extinction in conditioning of the rabbit's nictitating membrane response. *Psychobiology* **27**:85–94. doi:10.3758/BF03332102

Malone LA, Vasudevan EVL, Bastian AJ. 2011. Motor Adaptation Training for Faster Relearning. *J Neurosci* **31**:15136–15143. doi:10.1523/JNEUROSCI.1367-11.2011

Maris E, Oostenveld R. 2007. Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods* **164**:177–190. doi:10.1016/j.jneumeth.2007.03.024

Marko MK, Haith AM, Harran MD, Shadmehr R. 2012. Sensitivity to prediction error in reach adaptation. *Journal of Neurophysiology* **108**:1752–1763. doi:10.1152/jn.00177.2012

Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT. 1996. Throwing while looking through prismsI. Focal olivocerebellar lesions impair adaptation. *Brain* **119**:1183–1198. doi:10.1093/brain/119.4.1183

Mawase F, Shmuelof L, Bar-Haim S, Karniel A. 2014. Savings in locomotor adaptation explained by changes in learning parameters following initial adaptation. *Journal of Neurophysiology* **111**:1444–1454. doi:10.1152/jn.00734.2013

Mazzoni P, Krakauer JW. 2006. An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *J Neurosci* **26**:3642–3645. doi:10.1523/JNEUROSCI.5317-05.2006

McDougle SD, Bond KM, Taylor JA. 2017. Implications of plan-based generalization in sensorimotor adaptation. *Journal of Neurophysiology* **118**:383–393. doi:10.1152/jn.00974.2016

McDougle SD, Taylor JA. 2019. Dissociable cognitive strategies for sensorimotor learning. *Nature Communications* **10**:40. doi:10.1038/s41467-018-07941-0

Medina JF, Garcia KS, Mauk MD. 2001. A Mechanism for Savings in the Cerebellum. *J Neurosci* **21**:4081–4089. doi:10.1523/JNEUROSCI.21-11-04081.2001

Miall RC, Jenkinson N, Kulkarni K. 2004. Adaptation to rotated visual feedback: a re-examination of motor interference. *Exp Brain Res* **154**:201–210. doi:10.1007/s00221-003-1630-2

Milner B. 1962. Physiologie de l'Hippocampe: Colloque International, No. 107, Editions du Centre National de la Recherche Scientifique, Paris, 1962. 512 pp. 58NF. Pergamon.

Morehead JR, Qasim SE, Crossley MJ, Ivry R. 2015. Savings upon Re-Aiming in Visuomotor Adaptation. *J Neurosci* **35**:14386–14396. doi:10.1523/JNEUROSCI.1046-15.2015

Morehead JR, Taylor JA, Parvin DE, Ivry RB. 2017. Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience* **29**:1061–1074. doi:10.1162/jocn_a_01108

Napier RM, Macrae M, Kehoe EJ. 1992. Rapid reacquisition in conditioning of the rabbit's nictitating membrane response. *Journal of Experimental Psychology: Animal Behavior Processes* **18**:182–192. doi:10.1037/0097-7403.18.2.182

Nguyen-Vu TB, Zhao GQ, Lahiri S, Kimpo RR, Lee H, Ganguli S, Shatz CJ, Raymond JL. 2017. A saturation hypothesis to explain both enhanced and impaired learning with enhanced plasticity. *eLife* **6**:e20147. doi:10.7554/eLife.20147

Oh Y, Schweighofer N. 2019. Minimizing Precision-Weighted Sensory Prediction Errors via Memory Formation and Switching in Motor Adaptation. *J Neurosci* **39**:9237–9250. doi:10.1523/JNEUROSCI.3250-18.2019

Oldfield RC. 1971. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* **9**:97–113. doi:10.1016/0028-3932(71)90067-4

Pearce JM. 2013. Animal Learning and Cognition: An Introduction. Psychology Press.

Raibert MH. 1978. A model for sensorimotor control and learning. *Biol Cybernetics* **29**:29–36. doi:10.1007/BF00365233

Reichenthal M, Avraham G, Karniel A, Shmuelof L. 2016. Target size matters: target errors contribute to the generalization of implicit visuomotor learning. *Journal of Neurophysiology* **116**:411–424. doi:10.1152/jn.00830.2015

Rogers R, Monsell S. 1995. Costs of a Predictable Switch Between Simple Cognitive Tasks. *Journal of Experimental Psychology: General* **124**:207–231. doi:10.1037/0096-3445.124.2.207

Schlerf JE, Xu J, Klemfuss NM, Griffiths TL, Ivry RB. 2012. Individuals with cerebellar degeneration show similar adaptation deficits with large and small visuomotor errors. *Journal of Neurophysiology* **109**:1164–1173. doi:10.1152/jn.00654.2011

Schween R, McDougle SD, Hegele M, Taylor JA. 2020. Assessing explicit strategies in force field adaptation. *Journal of Neurophysiology* **123**:1552–1565. doi:10.1152/jn.00427.2019

Shadmehr R, Brashers-Krug T. 1997. Functional Stages in the Formation of Human Long-Term Motor Memory. *J Neurosci* **17**:409–419. doi:10.1523/JNEUROSCI.17-01-00409.1997

Smith MA, Ghazizadeh A, Shadmehr R. 2006. Interacting Adaptive Processes with Different Timescales Underlie Short-Term Motor Learning. *PLOS Biology* **4**:e179. doi:10.1371/journal.pbio.0040179

Srull TK. 1981. Person memory: Some tests of associative storage and retrieval models. *Journal of Experimental Psychology: Human Learning and Memory* **7**:440–463. doi:10.1037/0278-7393.7.6.440

Stark-Inbar A, Raza M, Taylor JA, Ivry RB. 2016. Individual differences in implicit motor learning: task specificity in sensorimotor adaptation and sequence learning. *Journal of Neurophysiology* **117**:412–428. doi:10.1152/jn.01141.2015

Steinmetz AB, Freeman JH. 2014. Localization of the cerebellar cortical zone mediating acquisition of eyeblink conditioning in rats. *Neurobiology of Learning and Memory* **114**:148–154. doi:10.1016/j.nlm.2014.06.003

Taylor JA, Klemfuss NM, Ivry RB. 2010. An Explicit Strategy Prevails When the Cerebellum Fails to Compute Movement Errors. *Cerebellum* **9**:580–586. doi:10.1007/s12311-010-0201-x

Taylor JA, Krakauer JW, Ivry RB. 2014. Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *J Neurosci* **34**:3023–3032. doi:10.1523/JNEUROSCI.3619-13.2014

Thoroughman KA, Shadmehr R. 2000. Learning of action through adaptive combination of motor primitives. *Nature* **407**:742–747.

Tsay Jonathan S., Lee AS, Avraham G, Parvin DE, Ho J, Boggess M, Woo R, Nakayama K, Ivry RB. 2020a. OnPoint: A package for online experiments in motor control and motor learning. PsyArXiv. doi:10.31234/osf.io/hwmpy

Tsay Jonathan S., Avraham G, Kim HE, Parvin DE, Wang Z, Ivry RB. 2020b. The effect of visual uncertainty on implicit motor adaptation. *Journal of Neurophysiology* **125**:12–22. doi:10.1152/jn.00493.2020

Tsay Jonathan S., Kim HE, Parvin DE, Stover AR, Ivry RB. 2020c. Individual differences in proprioception predict the extent of implicit sensorimotor adaptation. *bioRxiv* 2020.10.03.324855. doi:10.1101/2020.10.03.324855

Tsay Jonathan S., Parvin DE, Ivry RB. 2020d. Continuous reports of sensed hand position during sensorimotor adaptation. *Journal of Neurophysiology* **124**:1122–1130. doi:10.1152/jn.00242.2020

Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ. 2007. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* **98**:54–62. doi:10.1152/jn.00266.2007

Vandevoorde K, Orban de Xivry J-J. 2019. Internal model recalibration does not deteriorate with age while motor adaptation does. *Neurobiology of Aging* **80**:138–153. doi:10.1016/j.neurobiolaging.2019.03.020

Wei K, Körding K. 2009. Relevance of Error: What Drives Motor Adaptation? *Journal of Neurophysiology* **101**:655–664. doi:10.1152/jn.90545.2008

Weiner MJ, Hallett M, Funkenstein HH. 1983. Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. *Neurology* **33**:766–766. doi:10.1212/WNL.33.6.766

Wilterson SA, Taylor JA. 2020. Implicit visuomotor adaptation remains limited after several days of training. *bioRxiv* 711598. doi:10.1101/711598

Wong AL, Marvel CL, Taylor JA, Krakauer JW. 2019. Can patients with cerebellar disease switch learning mechanisms to reduce their adaptation deficits? *Brain* **142**:662–673. doi:10.1093/brain/awy334

Woodruff-Pak DS. 1993. Eyeblink classical conditioning in H. M.: Delay and trace paradigms. *Behavioral Neuroscience* **107**:911–925. doi:10.1037/0735-7044.107.6.911

Yin C, Wei K. 2020. Savings in sensorimotor adaptation without an explicit strategy. *Journal of Neurophysiology* **123**:1180–1192. doi:10.1152/jn.00524.2019

Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW. 2008. Explaining Savings for Visuomotor Adaptation: Linear Time-Invariant State-Space Models Are Not Sufficient. *Journal of Neurophysiology* **100**:2537–2548. doi:10.1152/jn.90529.2008

Zhou W, Fitzgerald J, Colucci-Chang K, Murthy KG, Joiner WM. 2017. The temporal stability of visuomotor adaptation generalization. *Journal of Neurophysiology* **118**:2435–2447. doi:10.1152/jn.00822.2016

Figure captions

Figure 1. Experiment 1: Upon relearning a visuomotor rotation, explicit strategies show savings while implicit adaptation is attenuated.

(**A**) Task-level schematics of all trial types. (**B**) Time course of mean hand angle averaged over cycles (4 movements) when participants (N=24) were asked to aim for the target (blue), either during No Feedback blocks (No FB Baseline and Aftereffect, gray background), Veridical Feedback blocks (FB Baseline and Washout), or no feedback Probe trials, and when asked to compensate for a rotated cursor (Rotation, pink). Light and dark colors signify blocks 1 and 2 of the experiment. Dotted vertical lines denote one (thin) and two (thick) min breaks. The labels 'Early' and 'Late' mark the cycles used for operationalizing measures of early and late learning. (**C**, **D**) To highlight changes across blocks, overlaid hand angle functions of blocks 1 and 2 for overall learning (explicit and implicit, Rotation trials, *C*) and implicit adaptation (Baseline, Probe and Aftereffect trials, *D*). Horizontal thick black lines mark clusters of cycles that show significant difference between the blocks with $p<0.05$ probability. Cycle numbers in both *C* and *D* correspond to the cycles of the Rotation trials. (**E-I**) Summary analysis of Early learning (*E*, *G*) and Late learning (*F*, *H*) for the Rotation (*E*, *F*) and Probe (*G*, *H*) conditions, and of the aftereffects (*I*). Left pair of bars show the mean across participants for each block, and right bar shows the mean of the within-participant differences (Block 2 – Block 1). Black dots indicate individual difference scores. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

Figure 2. Experiment 2: Task-irrelevant clamped feedback revealed an overall attenuation of implicit adaptation upon relearning.

(**A**) Task-level schematics of all trial types. (**B**) Experimental protocol of two experimental groups: Test (N=16, green) and Control (N=16, purple). For the Test group, the green oblique lines in the Washout block represent a transition from a reversed-clamp phase to a veridical feedback phase; the cycle of the transition was determined based on each individual's performance in the reversed-clamp phase (see Methods). (**C**) Time courses of mean hand angle averaged over cycles (4 movements) for both groups. For the Test group, light and dark green colors signify blocks 1 and 2 of the experiment, with the onset of the task-irrelevant clamped feedback marked by the vertical solid lines. Dotted vertical lines denote one (thin) and two (thick) min breaks. The labels 'Early' and 'Late' mark the cycles used for operationalizing measures of early and late learning. (**D**) Overlaid hand angle functions for the two blocks. Horizontal thick black lines denote clusters that show a significant difference between blocks 1 and 2 ($p<0.05$). (**E-H**) Summary analysis of Early learning (*E*), Late learning (*F*) and Aftereffect (*G*) stages for the Test group, and Late learning for the Control group (*H*). Left pair of bars show the mean across participants for each block, and right bar shows the mean of the within participant differences Block 2 – Block 1. Black dots indicate individual difference scores. (**I**) Summary analysis comparing the Aftereffect between the groups in the last No FB block. Black dots represent data of individual participants. (**J**) Overlaid hand angle functions for the Aftereffect block of the Control group and the Aftereffect 1 (left panel) or Aftereffect 2 (right panel) of the Test group. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

Figure 3. Prior evidence for attenuation upon relearning for implicit visuomotor adaptation.

(**A**) Cohen's *d* effect size of the differences in learning measures between the second and first learning blocks for experiments meeting our criterion for inclusion in the review of the literature. Early learning (green circles), Late learning (blue triangles), Aftereffect (purple squares) and Learning rate (dark purple stars). (**B, C**) Overlaid hand angle functions of implicit adaptation to a

visuomotor rotation over two learning blocks separated by a washout phase (not shown). Light and dark colors denote blocks 1 and 2 of the experiment, respectively. Shaded margins represent the SEM. In **B**, implicit adaptation was extracted by subtracting a reported aiming location from movement hand angle on every trial. Adapted with permission from Yin and Wei, 2020. In **C**, implicit adaptive response to the rotated cursor when the target jumps in a manner that eliminates task error. Adapted with permission from Leow et al., 2020. (**D**) Learning rate during adaptation to a gradually changing visuomotor rotation, tested on two days. Pink markers represent individual participants. Black diagonal dotted line represents the unity line. Bars and black vertical lines (inset) represent mean and SEM, respectively. Adapted with permission from Stark-Inbar et al., 2016.

Figure S1. Experiment 1: Strategy switching between Rotation and Probe trials

Hand angle for each trial in Rotation-Probe-Rotation triplets, highlighting the switching behavior for each participant (grey lines) between the Rotation (pink dots) and Probe trials (blue dots). The horizontal dashed grey line represents full compensation for 45° visuomotor rotation. The data are shown for early and late stages of the two learning blocks. The mean values (squares) increase from early to late, and within the early phase, between the first and second block on Rotation trials, indicative of overall learning and savings, respectively.

Figure S2. Experiment 2S: Replication study using an online crowdsourcing platform.

(**A**) Time course of participants' (N=48) mean hand angle averaged over cycles, showing robust adaptation to the task-irrelevant clamped feedback (onset marked by the vertical lines) in blocks 1 (light green) and 2 (dark green) (Early-Late Stage main effect: $F(1,47)=90.8$, $p<0.001$, $\eta_p^2=0.66$). (**B**) Overlaid hand angle functions for the two blocks, showing attenuation in multiple clusters

throughout the learning and aftereffect blocks ($p<0.05$). While the effect of Block was not significant ($F(1,47)=1.09$, $p=0.302$, $\eta_p^2=0.02$), there was a significant Stage x Block interaction effect ($F(1,47)=4.99$, $p=0.030$, $\eta_p^2=0.10$). (**C-D**) The interaction reflects the finding that there was a significant attenuation in the Late stage (-1.57°±0.74°, $t(47)=-2.14$, $p=0.038$, BF10=1.25, $d=-0.31$), but no difference in the Early stage (0.58°±0.61°, $t(47)=0.950$, $p=0.347$, BF10=0.240, $d=0.14$). (**E**) Similar to the results of Experiments 1 and 2, marked attenuation was observed in the Aftereffect stage (-3.35°±0.81°, $t(47)=-4.14$, $p<0.001$, BF10=168, $d=-0.60$). For panels *C-E*, the left pair of bars show the mean across participants for each block, and the right bar shows the mean of the within-participant differences Block 2 – Block 1. Black dots indicate individual difference scores. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

Figure 1

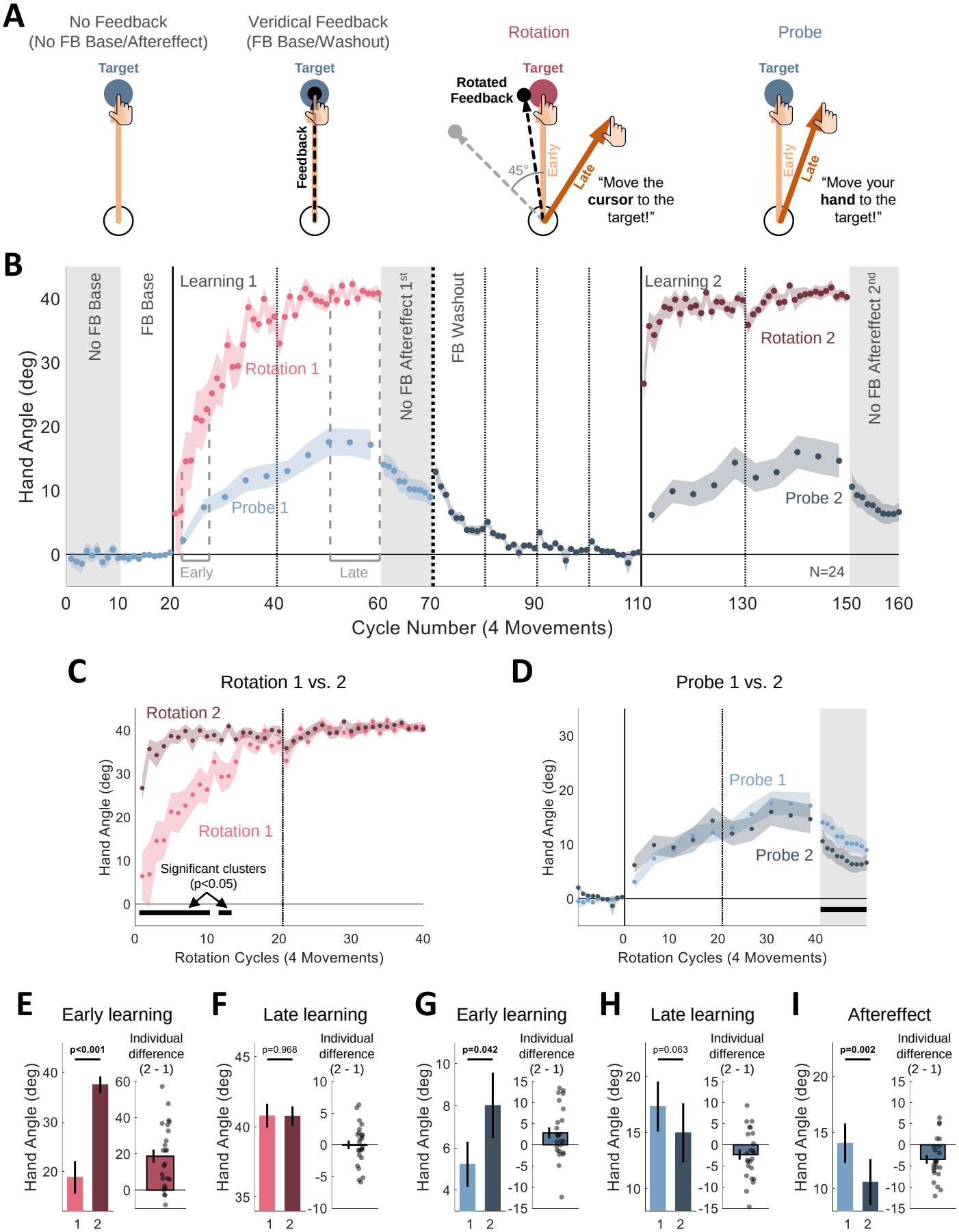

A
No Feedback
(No FB Base/Aftereffect)
Veridical Feedback
(FB Base/Washout)
Rotation
Probe
Target
Feedback
Rotated Feedback
45°
Early
Late
"Move the cursor to the target!"
"Move your hand to the target!"
B
No FB Base
FB Base
Learning 1
Rotation 1
Probe 1
No FB Aftereffect 1st
FB Washout
Learning 2
Rotation 2
Probe 2
No FB Aftereffect 2nd
Early
Late
N=24
Hand Angle (deg)
Cycle Number (4 Movements)
C
Rotation 1 vs. 2
Rotation 2
Rotation 1
Significant clusters
(p<0.05)
Hand Angle (deg)
Rotation Cycles (4 Movements)
D
Probe 1 vs. 2
Probe 1
Probe 2
Hand Angle (deg)
Rotation Cycles (4 Movements)
E
Early learning
p<0.001
Individual difference (2 - 1)
F
Late learning
p=0.968
Individual difference (2 - 1)
G
Early learning
p=0.042
Individual difference (2 - 1)
H
Late learning
p=0.063
Individual difference (2 - 1)
I
Aftereffect
p=0.002
Individual difference (2 - 1)
Hand Angle (deg)

Figure 2

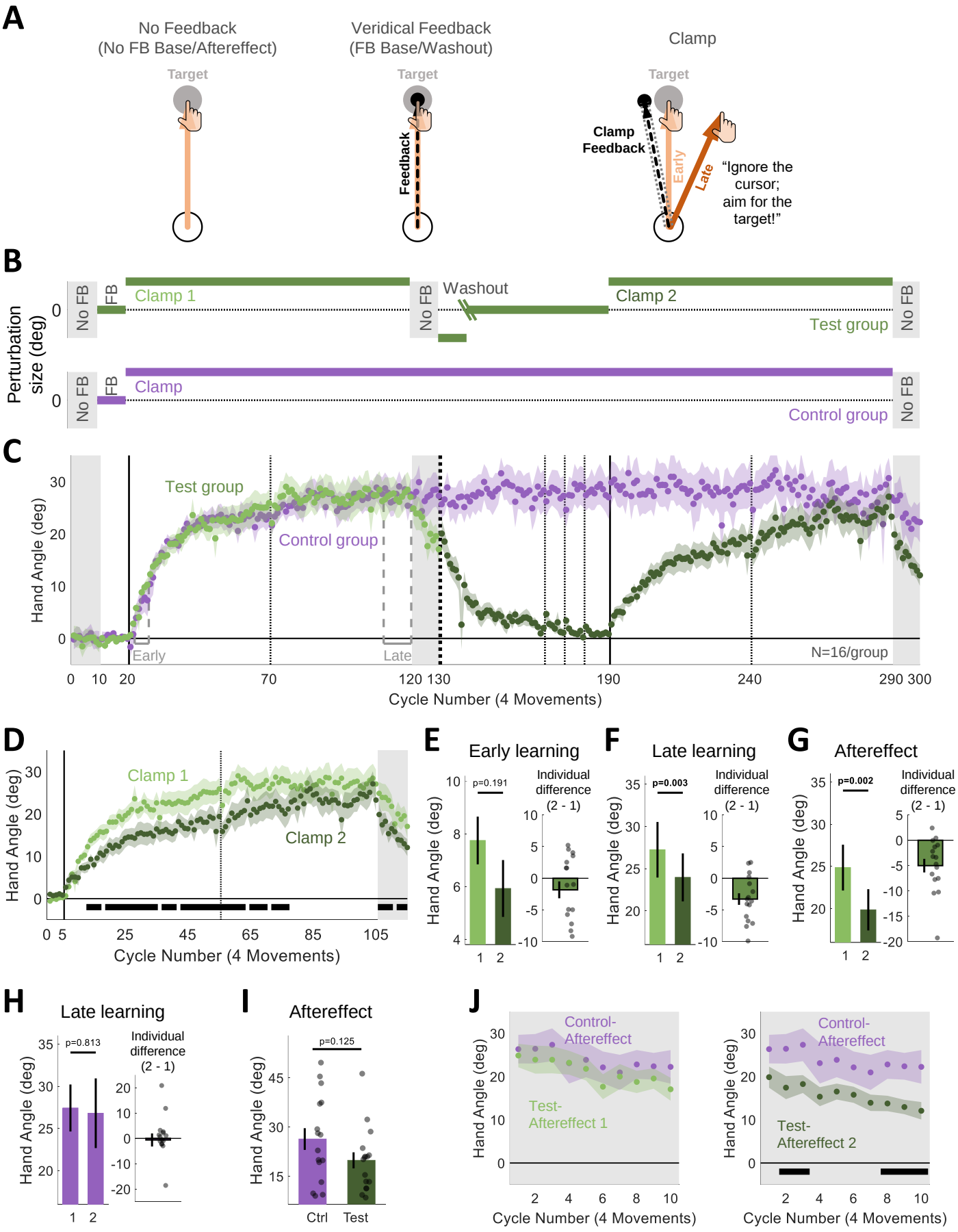
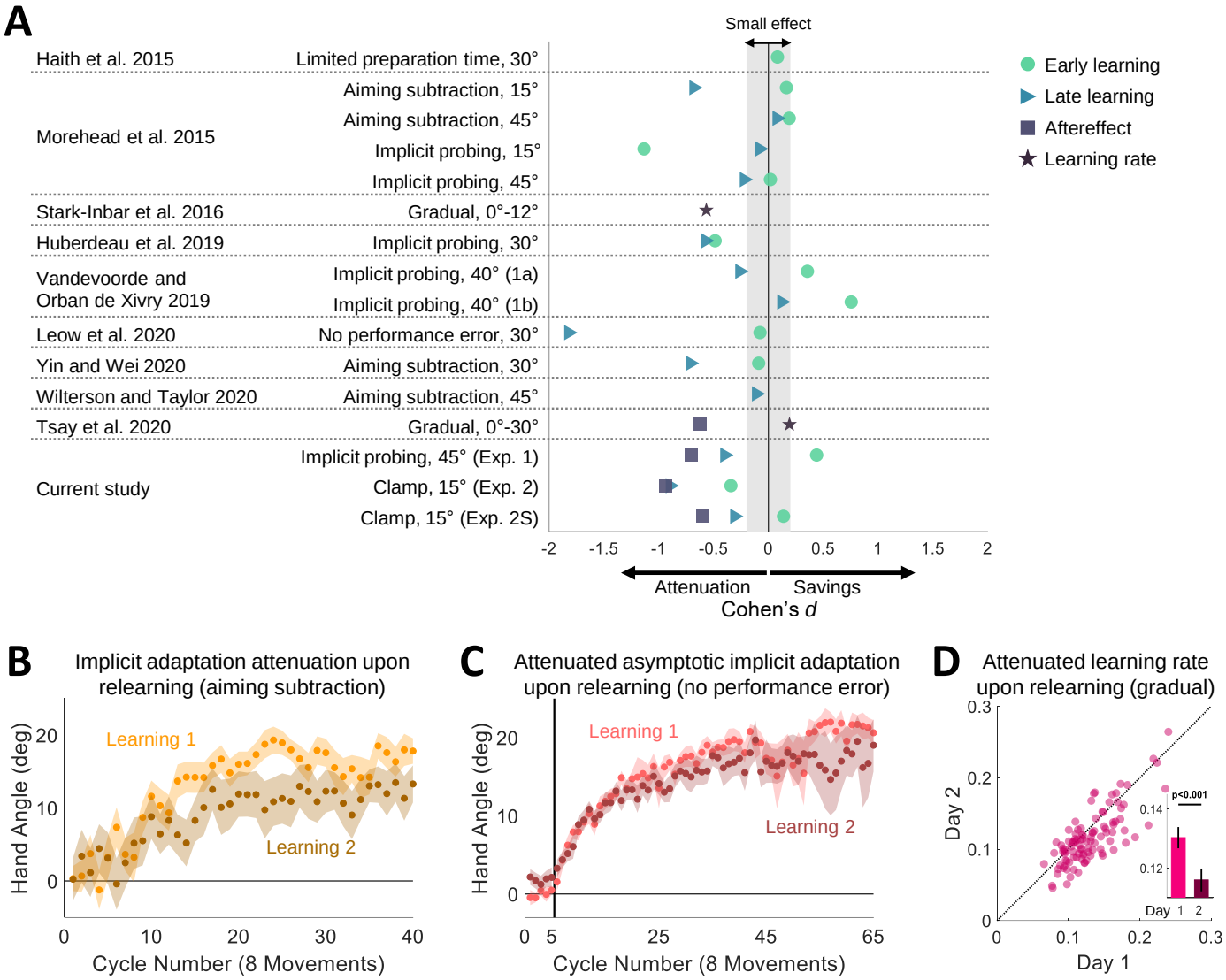

A
No Feedback
(No FB Base/Aftereffect)
Veridical Feedback
(FB Base/Washout)
Clamp
Target
Feedback
Clamp
Feedback
Early
Late
"Ignore the cursor; aim for the target!"
B
Perturbation size (deg)
No FB
FB
Clamp 1
Washout
Clamp 2
Test group
Clamp
Control group
C
Hand Angle (deg)
Test group
Control group
Early
Late
N=16/group
Cycle Number (4 Movements)
D
Clamp 1
Clamp 2
Cycle Number (4 Movements)
E
Early learning
p=0.191
Individual difference (2 - 1)
F
Late learning
p=0.003
G
Aftereffect
p=0.002
H
Late learning
p=0.813
I
Aftereffect
p=0.125
Ctrl
Test
J
Control-Aftereffect
Test-Aftereffect 1
Test-Aftereffect 2
Cycle Number (4 Movements)

Figure 3


A
Small effect
Haith et al. 2015
Limited preparation time, 30°
Morehead et al. 2015
Aiming subtraction, 15°
Aiming subtraction, 45°
Implicit probing, 15°
Implicit probing, 45°
Stark-Inbar et al. 2016
Gradual, 0°-12°
Huberdeau et al. 2019
Implicit probing, 30°
Vandevoorde and Orban de Xivry 2019
Implicit probing, 40° (1a)
Implicit probing, 40° (1b)
Leow et al. 2020
No performance error, 30°
Yin and Wei 2020
Aiming subtraction, 30°
Wilterson and Taylor 2020
Aiming subtraction, 45°
Tsay et al. 2020
Gradual, 0°-30°
Current study
Implicit probing, 45° (Exp. 1)
Clamp, 15° (Exp. 2)
Clamp, 15° (Exp. 2S)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Attenuation
Savings
Cohen's d
Early learning
Late learning
Aftereffect
Learning rate
B
Implicit adaptation attenuation upon relearning (aiming subtraction)
Learning 1
Learning 2
Hand Angle (deg)
Cycle Number (8 Movements)
C
Attenuated asymptotic implicit adaptation upon relearning (no performance error)
Learning 1
Learning 2
Hand Angle (deg)
Cycle Number (8 Movements)
D
Attenuated learning rate upon relearning (gradual)
Day 2
Day 1
p<0.001
Day 1 2