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

Short title: Implicit adaptation is attenuated upon re-learning

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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. The initial rate of learning, a measure encompassing both processes, was faster in the second exposure to the perturbation. Surprisingly, the overall level of implicit adaptation was lower during relearning. Moreover, 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. These results provide evidence 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;

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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. 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

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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 provide assays solely of the state of implicit

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adaptation (Huberdeau et al., 2019; Morehead et al., 2015; Vandevoorde and Orban de Xivry, 2019).

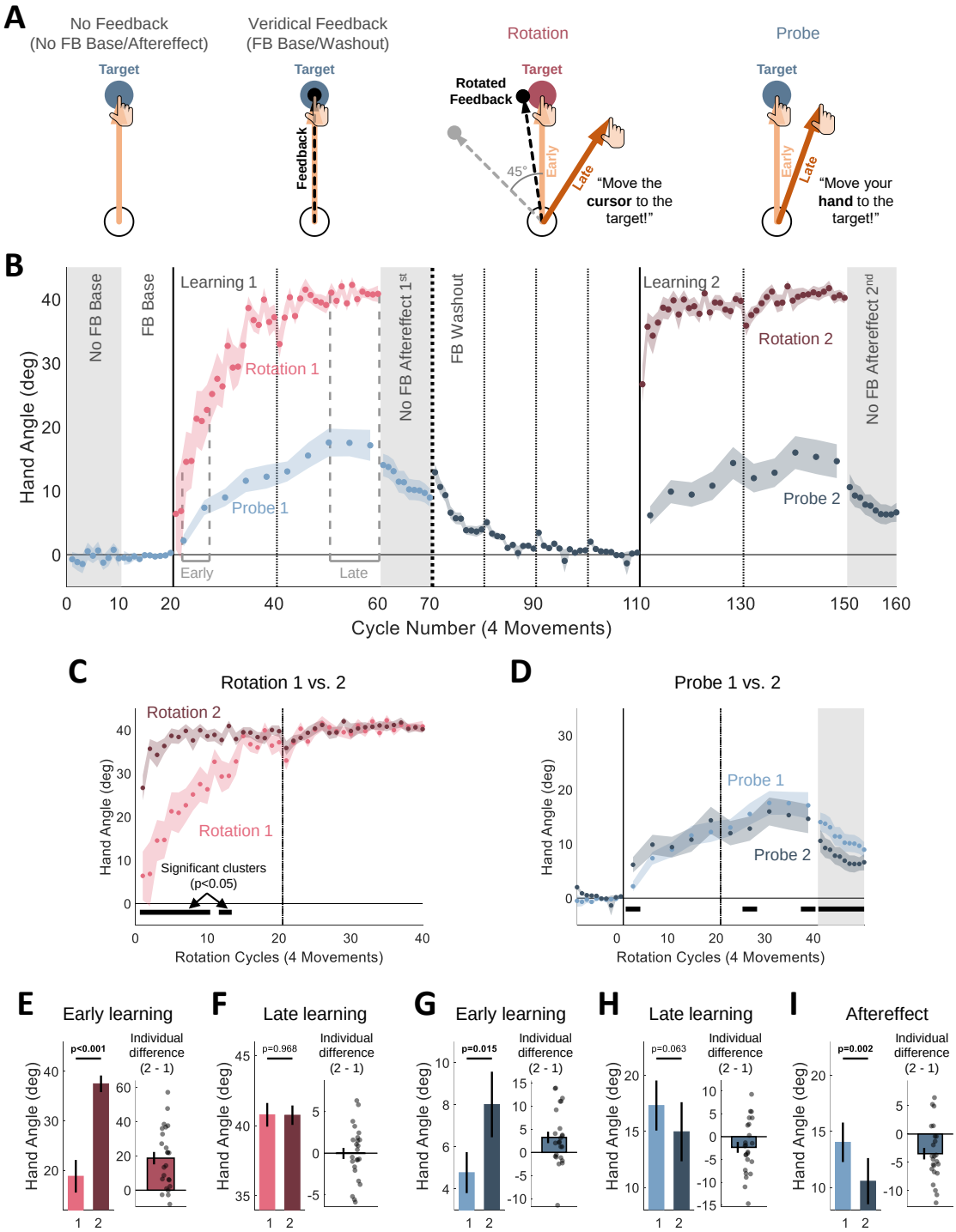

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Figure 1. Experiment 1: Upon relearning a visuomotor rotation, explicit strategies show savings while implicit adaptation is attenuated.

(**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**) Mean hand angle time courses of the two sessions overlaying one another for the overall learning (explicit and implicit, Rotation trials, *C*) and implicit (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 panels show the mean across participants for each block, and right panels the mean of the within participants' differences between the 2nd and 1st learning blocks. Semi-transparent colored dots represent the individuals' differences. 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, getting close (~40°) to the ideal 45° change in hand angle by the end of the block (Fig. 1B). The hand angle was also shifted in the same direction on probe trials, despite the instructions to reach directly to the target. This shift was markedly less than that observed on the rotation trials, with a mean shift of ~17° by the end of the learning block. The behavioral changes observed during the probe trials reflect the extent of implicit learning, which sums with explicit aiming during the rotation trials.

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).

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Marked savings was observed on the rotation trials: Performance improved at a faster rate relative to the first learning block (Fig. 1C). We used two approaches to statistically evaluate the data. One analysis examined the 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). There was a significant increase in Early learning in the second learning block ($t(23) = 5.16$, $\mathrm{p} < 0.001$, $\mathrm{BF}_{10} = 775$, Fig. 1E), indicative of savings. The two blocks did not differ in the Late comparison ($\mathrm{t}(23) = 0.04$, $\mathrm{p} = 0.968$, $\mathrm{BF}_{10} = 0.215$, Fig. 1F), with performance in both learning blocks near asymptote during these cycles. 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). 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 (significant clusters at cycles 1-10 and 12-13, $p < 0.05$, Fig. 1C), consistent with the pre-defined analysis.

A more complex pattern was observed when analyzing the probe trials (Fig. 1D). When comparing performance in the first two cycles of probe trials, the change in hand angle was also faster in the second learning block ($t(23) = 2.62$, $p = 0.015$, $BF_{10} = 3.38$, Fig. 1G). However, this effect did not persist beyond the first probe cycle and even reversed, with the mean hand angle being marginally smaller at the end of the second learning block compared to the end of the first learning block ($t(23) = -1.96$, $p = 0.063$, $BF_{10} = 1.09$, Fig. 1H). In the cluster analysis, the reversal was significant, with the hand angle larger on cycle 1 of the Probe trials in the second learning block but reaching smaller values in cycles 7 and 10 of the second block ($p < 0.05$).

In addition to the probe trials, we also quantified implicit learning following each learning block with an aftereffect block in which the visual feedback was withheld and participants were reminded to reach directly to the target. Consistent with the results from the end of the learning blocks, the

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aftereffect was weaker after the second block compared to the first in a predefined analysis restricted to the first cycle of each aftereffect block ($t(23) = -3.43$, $p = 0.002$, $BF_{10} = 17.2$, Fig. 1I), and, as evident in the cluster analysis, persisted across the entire aftereffect block.

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 ($695 \pm 46\, ms$) compared to Rotation 1 ($858 \pm 74\, ms$) trials ($t(23) = -2.93$, $p = 0.007$, $BF_{10} = 6.21$). 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 two learning blocks for the probe trials ($\sim 670\, ms$ in both blocks, $t(23) = 0.008$, $p = 0.993$, $BF_{10} = 0.215$) and the two aftereffect blocks ($\sim 440\, ms$, $t(23) = 1.53$, $p = 0.140$, $BF_{10} = 0.595$).

The aftereffect data suggest that implicit adaptation is attenuated upon re-exposure of a perturbation. We considered two alternative hypotheses. 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 (1st aftereffect: $13.6 \pm 1.7\, s$; 2nd aftereffect: $12.4 \pm 1.7\, s$; $t(23) = -0.710$, $p = 0.485$, $BF_{10} = 0.270$). 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). Late in learning, the mean hand angle is similar on Rotation trials between the learning blocks and is ~2° lower on Probe trials of the second learning block. This may suggest that the

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aiming location is shifted farther from the target at the end of second block (thus resulting in similar overall performance). This raises the possibility that the reduced aftereffect is due to the measure being taken at the target location, a point that that would be farther along a generalization function centered at aiming location. Estimates of Gaussian generalization functions in the literature (e.g., McDougle et al., 2017) provide a means to evaluate this hypothesis: 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. Experiment 2 addresses this issue in a different way, using a method in which aiming remains at the target throughout the entire experiment (see below).

The results of Experiment 1 provide clear evidence of savings. Consistent with previous studies (Haith et al., 2015; Morehead et al., 2015), savings was most evident in the early cycles of the rotation trials, where the largest component to learning comes from the use of an explicit aiming strategy. In contrast, we observed a mixed pattern for implicit adaptation on probe trials: The change in hand angle was larger early on in the second learning block, but this advantage was transient and eventually reversed such that overall, implicit adaptation was attenuated upon relearning. The clearest evidence of this attenuation was observed in the aftereffect data.

The faster increase in hand angle over the first cycles of the probe trials in the second learning block might also be taken as evidence of savings. However, it is also important to keep in mind that the design of Experiment 1 required participants to frequently switch strategy (Rogers and Monsell, 1995): During the rotation trials, participants learned to aim away from the target, whereas in probe trials, they were instructed to aim directly to the target. Since the aiming strategies are larger during the second learning block, failures to completely dispense with the

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aiming strategy would contaminate the probe trials in a way that would make it appear as if they exhibit savings.

To obtain a purer assay of the contribution of implicit adaptation to savings, 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, the change in hand angle in response to clamped visual feedback is implicit, an inference supported by converging evidence from other measures of adaptation (Morehead et al., 2017; Tsay et al., 2020). Since the participant is instructed to always aim at the target, this experiment also addresses concerns in Experiment 1 related to the effects of aim-based generalization.

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). Reaction times were uniformly fast ($\sim 400\ ms$), consistent with the hypothesis that participants aim directly to the target, and were similar during the first and second learning blocks (Clamp trials: $t(15) = -0.359$, $p = 0.725$, $BF_{10} = 0.271$; Aftereffect trials: $t(15) = 0.063$, $p = 0.951$, $BF_{10} = 0.256$).

Interestingly, the adaptation function was markedly attenuated in the second learning block (Fig 2D). Unlike the probe trials of Experiment 1, early re-adaptation did not increase, and even were numerically lower ($t(15) = -1.37$, $p = 0.191$, $BF_{10} = 0.562$, Fig. 2E). This attenuation was clearly evident in the analyses involving predefined cycles for Late learning ($t(15) = -3.59$, $p = 0.003$, $BF_{10} = 16.3$, Fig. 2F) and Aftereffect: ($t(15) = -3.74$, $p = 0.002$, $BF_{10} = 21.5$, Fig. 2G), and

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205 across multiple cycles in the cluster analysis ($p < 0.05$, Fig. 2D). Thus, the results clearly argue
206 against savings of implicit adaptation, and provide direct evidence that this learning process is
207 attenuated upon relearning.

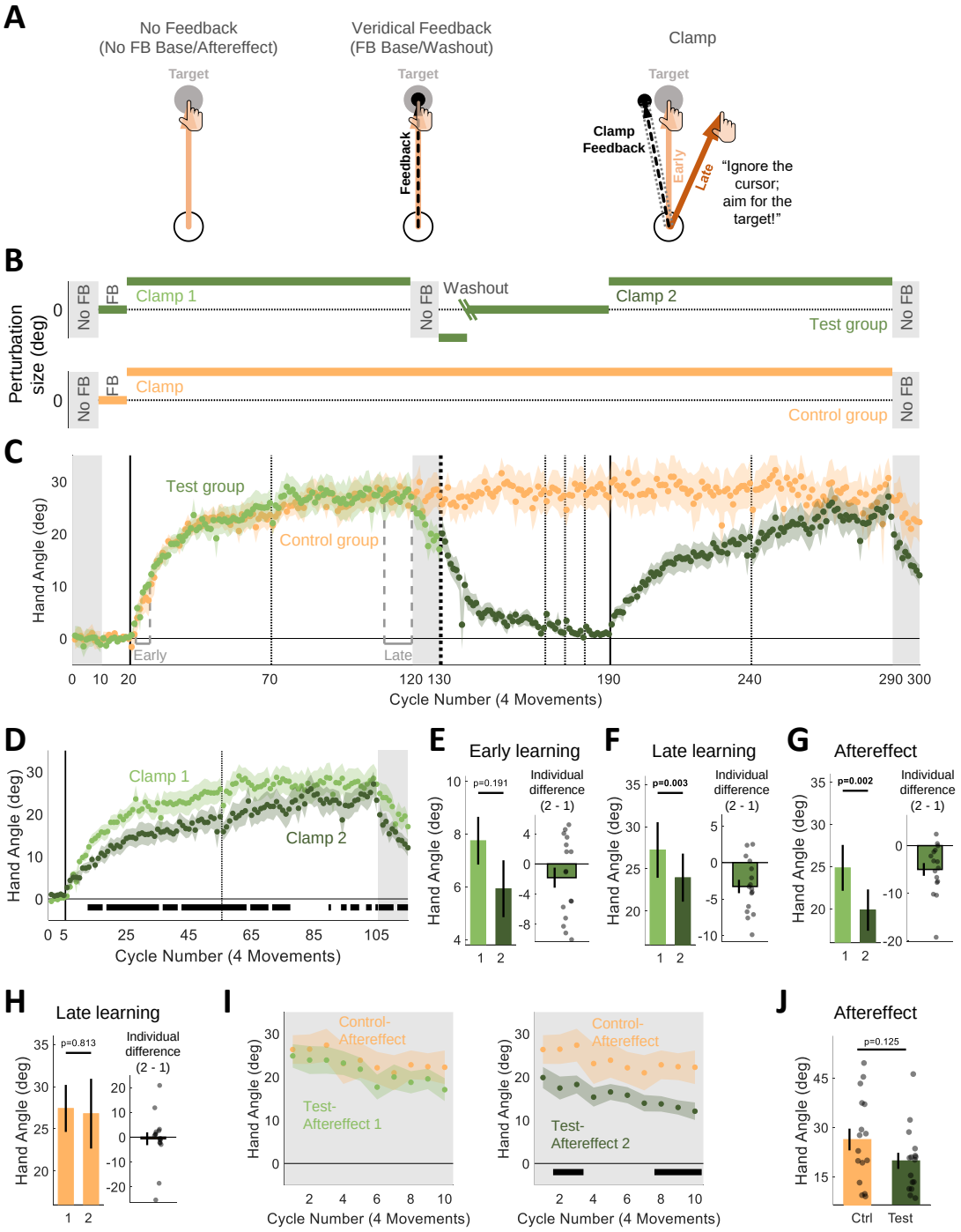

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Figure 2. Experiment 2: Task-irrelevant clamped feedback revealed an overall attenuation of implicit adaptation upon relearning.

(**A**) Task-level schematics of all trial types. (**B**) Experimental protocol of two experimental groups: Test (N=16, green) and Control (N=16, orange). 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. 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. (**D**) Mean hand angle time courses of the two sessions overlaying one another. Horizontal thick black lines mark clusters of cycles that show significant difference between the blocks with $p<0.05$ probability. (**E-H**) Summary analysis of Early learning (*E*), Late learning (*F*) and Aftereffect (*G*) for the Test group, and Late learning for the Control group (*H*). Left panels show the mean across participants for each block, and right panels the mean of the within participants' differences between the 2nd and 1st learning blocks. Semi-transparent colored dots represent the individuals' differences. (**I**) Mean hand angle time courses during the Aftereffect block of the Control group overlaying the Aftereffect 1 (left panel) or Aftereffect 2 (right panel) blocks of the Test group. (**J**) Summary analysis comparing the Aftereffect between the groups in the last No FB block. Colored dots represent data of individual participants. For all figure panels, shaded margins and black vertical lines represent standard error of the mean (SEM).

We considered the possibility that the attenuation of adaptation 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, $t(15) = -0.24$, $p = 0.813$, $BF_{10} = 0.262$, Fig. 2H).

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In direct comparisons of the two groups using the cluster analysis, the hand angle of the Control group in the aftereffect block (only one such block, cycles 291-300) did not defer from that of the Test group in their first aftereffect block (cycles 121-130) (Fig 2I, left panel). Thus, the Control group did not show any attenuation in adaptation over time. However, adaptation was larger for the Control group compared to the Test group in their second aftereffect block (cycles 291-300). Although this contrast was not significant in the pre-defined analysis of the first aftereffect cycle ($t(30) = 1.58$, $p = 0.125$, $BF_{10} = 0.857$, Fig. 2J), the cluster-based analysis revealed significant effects in five of the ten cycles (clusters in cycles 2-3 and 8-10, $p < 0.05$, Fig. 2I, right panel). These results indicate that the attenuation of implicit adaptation takes place specifically upon relearning, and is not attributable to fatigue or habituation.

This attenuation of implicit learning, observed in both Experiments 1 and 2, was surprising given that past studies have presented evidence showing savings (Coltman et al., 2019; Yin and Wei, 2020). Despite several studies showing no savings (Haith et al., 2015; Leow et al., 2020; Morehead et al., 2015), we were unaware of any prior reports of attenuation in implicit adaptation. However, as noted in our motivation for Experiment 2, it can be difficult to obtain “pure” measures of implicit learning with most of the methods used to study sensorimotor adaptation. With this caveat in mind, we reviewed the sensorimotor learning literature, focusing on studies that employed designs in which these methodological limitations would be less relevant.

To our surprise, we found several studies that also show attenuation of implicit adaptation upon relearning. In an individual difference study from our lab, participants were tested on a variety of implicit learning tasks, each repeated over two sessions. 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 significantly lower on the second day (Stark-Inbar et al., 2016) (Fig. 3A). Another study asked whether explicit and implicit learning processes improve across experimental sessions that alternated between

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clockwise and counterclockwise rotations (Huberdeau et al., 2019). The results showed improvement in explicit strategies across days even with limited preparation time, consistent with the idea that the strategy use becomes more automatic with practice (McDougle and Taylor, 2019). Using interleaved no-feedback trials in a design similar to that used in Experiment 1 here, the data also showed a decrease in implicit adaptation, although the authors emphasized this effect as 'no improvement'.

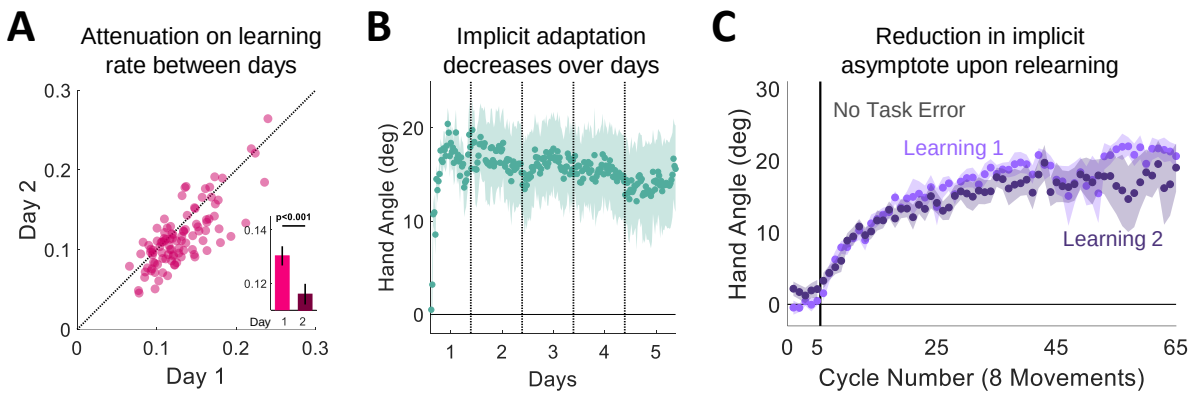

Figure 3. Prior evidence for attenuation upon relearning for implicit visuomotor adaptation.

(**A**) Learning rate during adaptation to gradually changing visuomotor rotation over 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. (**B**) Mean hand angle time course of implicit adaptation to visuomotor rotation over five days (separated by black vertical dotted lines). Implicit adaptation here was extracted by subtracting a reported aiming location from movement hand angle on every trial. Shaded margins represent the SEM. Adapted with permission from Wilterson and Taylor, 2020. (**C**) Results from visuomotor rotation experiments, where a target jumps in a manner that eliminates task error. The time courses of mean hand angle over two rotation blocks (originally separated by washout) overlaying one another. Light and dark purple signify learning blocks 1 and 2 of the experiment, respectively. Shaded margins represent the SEM. Adapted with permission from Leow et al., 2020.

Attenuation of implicit adaptation is also observed in studies that have required participants to explicitly report their aiming location, and thus allowed estimates to be made of implicit adaption

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by taking the difference between the actual hand angle and the reported aiming location (Taylor et al., 2014). In one study (Wilterson and Taylor, 2020; see also Yin and Wei, 2020), this aiming report task was repeated over multiple days with a 45° rotation. The estimate of implicit adaptation decreased over days (Fig. 3B). Interestingly, there was no washout in this study. Superficially this might seem at odds with the data from the Control group in Experiment 2. However, there was an over-night break between sessions, necessitating some degree of relearning each day.

Lastly, Leow et al. (Leow et al., 2020) used a different method to isolate implicit learning, displacing the target during the reach such that it intersects the perturbed cursor (and thus eliminates task error). Here, too, the amount of implicit adaptation was reduced when the task was repeated after a washout block (Fig. 3C).

In summary, this review of the relevant published studies reveals a consistent attenuation of implicit adaptation upon relearning when this process can be clearly isolated. This phenomenon has been overlooked or, at most, briefly noted, because the issue was of secondary interest to the main goals of each study.

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 strategy

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use, but not other component processes including implicit sensorimotor adaptation (Haith et al., 2015; Morehead et al., 2015). Our results go beyond this observation, indicating that implicit adaption not only fails to exhibit savings, but is actually attenuated upon relearning. Our review of the literature indicates that this effect, despite being overlooked, is quite robust, at least with respect to visuomotor adaptation. 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.

Explicit and implicit processes upon relearning

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 presence 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).

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One recent study has shown that engaging the implicit system in an initial learning block with either a gradual visuomotor rotation or clamped visual feedback will increase the rate of learning in response to a subsequent abrupt 30° rotation (Yin and Wei, 2020). While the behavior here is indicative of savings (relative to control groups who did not receive the initial training), it is not clear that the savings come 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 large, salient error at the start of washout which might impact behavior in the second learning block. Interestingly, the same paper also included an experiment in which an aiming report task was used in a standard savings design (Yin and Wei, 2020). Their data also indicate that implicit adaptation, estimated by subtracting the aim reports from the actual hand position, was attenuated in the second block.

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; Steinmetz and Freeman, 2014; Woodruff-Pak, 1993) and in saccade adaptation (Kojima et al., 2004).

Possible mechanisms for attenuation upon relearning

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We consider two general explanations for an attenuation of relearning rate. We first consider how attenuation could come about from the modulation of parameters governing how the memory of a single representation is updated after each movement. We then turn to hypotheses in which attenuation reflects the interplay of multiple memory representations.

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; 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

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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 (VOR) 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 release synapses 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; Wilterson and Taylor, 2020) seems problematic for this unitary representation hypothesis.

An alternative framework for understanding attenuation during re-learning is to consider how learning functions may be modulated by the interplay of multiple representations. 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,

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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; Nguyen-Vu et al., 2017; 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 eyeblink conditioning (Frey and Butler, 1977) and appetitive conditioning (Bouton et al., 2004) if the extinction phase involves the repeated presentation of both the CS and US, but now in an unpaired manner. Theoretically, in these manipulations, the reversed rotation or decoupling of the CS-US relationship, lead to the establishment of a new representation, 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 (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 representations, 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 Experiment 2. These manipulations would be conducive sources of interference (e.g., extended association with

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veridical feedback in the experimental context). We do note that the multi-session study of Wilterson and Taylor (Wilterson and Taylor, 2020) does not fit easily with this account of attenuation, given that they did not include a washout phase. However, interference in their study 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 representation, 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 representations remains a question for future study.

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Methods

Participants

Fifty-six healthy volunteers (aged 18-40 years; 42 females) participated, 24 in Experiment 1 and 32 in Experiment 2. All were right-handed, as verified with the Edinburgh Handedness Inventory (Oldfield, 1971). The numbers for each experiment was chosen to provide good statistical power based on effect sizes documented in the literature (Morehead et al., 2015, 2017), and to ensure appropriate counter-balancing of the perturbation direction and target location sets. The protocol was approved by the Institutional Review Board at the University of California, Berkeley.

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

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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 at 45° (0° being the positive edge of the abscissa), 135°, 225°, 335° for half of the participants and 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 $132 \pm 4.16\, ms$ (±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 $1.69 \pm 0.05\, s$.

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.

<u>Experiment 1</u>

24 participants were tested in Experiment 1. The experimental session consisted of 180 movement cycles, each involving four movements, one to each target. 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 (30 cycles), Learning 2 (50 cycles) and Aftereffect 2 (10 cycles). The initial baseline blocks were included to

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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. The direction of the rotation (clockwise or counterclockwise) was fixed for a given participant and counterbalanced across participants. On these 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 instructions either above or below the center of the screen, with the position selected 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

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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. 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).

Experiment 2

Participants in Experiment 2 were assigned to either the Test (N=16) or Control (N=16) condition. 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

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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.

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 3° of the target for three 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. Importantly, 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. 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

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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) the washout block (cycles 167, 174 and 181).

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

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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).

All trials were included in the analysis. 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).

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 the 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

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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 operationalize the dependent variables of interest (Early learning, Late learning, Aftereffect). To examine within-participant changes in behavior between the two learning blocks, paired-sample *t* tests were used for each measure. A paired-sample *t* test was used in Experiment 2 to evaluate changes in asymptotic performance over time in the Control group, using cycles corresponding to late stages of Clamp 1 and Clamp 2 of the Test group. An independent two-sample *t* test was used to compare the aftereffect for the Test and Control groups, using the data from Aftereffect 2 for the Test group. Two-tailed t-tests were used for all of these analyses, with the statistical significance threshold set at the $p < 0.05$. For all comparisons, we also report 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).

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-

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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. When the original data set yielded multiple clusters, we sorted the clusters in a descending order according to their t-sums values, and tested each of them against the corresponding null distributions (e.g., the second cluster was compared to the null distribution of the second largest t-sum values in the permuted data). In Experiment 2, a similar 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.

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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**) Mean hand angle time courses of the two sessions overlaying one another for the overall learning (explicit and implicit, Rotation trials, *C*) and implicit (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 panels show the mean across participants for each block, and right panels the mean of the within participants' differences between the 2nd and 1st learning blocks. Semi-transparent colored dots represent the individuals' differences. 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.

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(**A**) Task-level schematics of all trial types. (**B**) Experimental protocol of two experimental groups: Test (N=16, green) and Control (N=16, orange). 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. 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. (**D**) Mean hand angle time courses of the two sessions overlaying one another. Horizontal thick black lines mark clusters of cycles that show significant difference between the blocks with $p<0.05$ probability. (**E-H**) Summary analysis of Early learning (*E*), Late learning (*F*) and Aftereffect (*G*) for the Test group, and Late learning for the Control group (*H*). Left panels show the mean across participants for each block, and right panels the mean of the within participants' differences between the 2nd and 1st learning blocks. Semi-transparent colored dots represent the individuals' differences. (**I**) Mean hand angle time courses during the Aftereffect block of the Control group overlaying the Aftereffect 1 (left panel) or Aftereffect 2 (right panel) blocks of the Test group. (**J**) Summary analysis comparing the Aftereffect between the groups in the last No FB block. Colored dots represent data of individual participants. 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**) Learning rate during adaptation to gradually changing visuomotor rotation over 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. (**B**) Mean hand angle time course of implicit adaptation

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to visuomotor rotation over five days (separated by black vertical dotted lines). Implicit adaptation here was extracted by subtracting a reported aiming location from movement hand angle on every trial. Shaded margins represent the SEM. Adapted with permission from Wilterson and Taylor, 2020. (**C**) Results from visuomotor rotation experiments, where a target jumps in a manner that eliminates task error. The time courses of mean hand angle over two rotation blocks (originally separated by washout) overlaying one another. Light and dark purple signify learning blocks 1 and 2 of the experiment, respectively. Shaded margins represent the SEM. Adapted with permission from Leow et al., 2020.

Figure 1

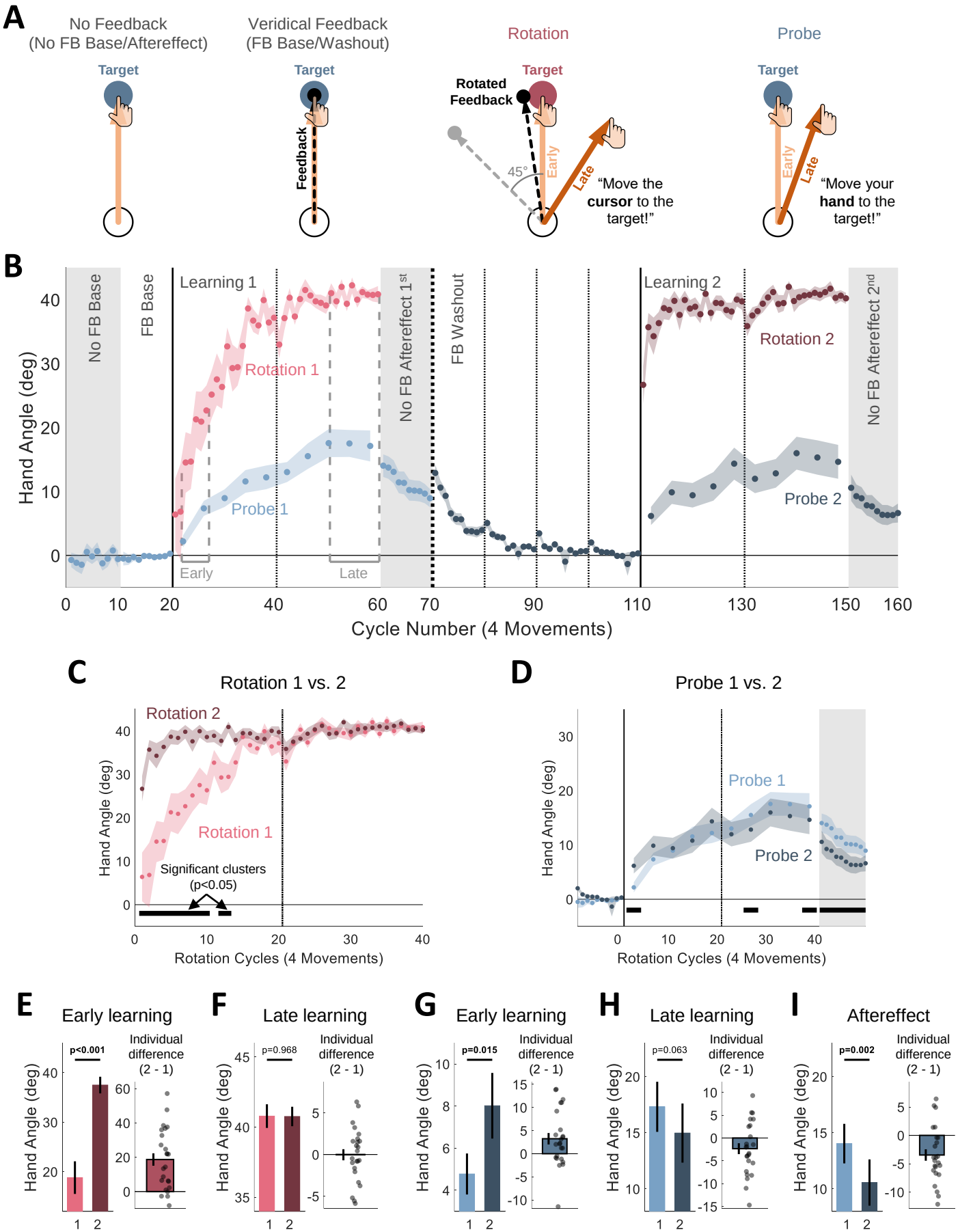

A
No Feedback
(No FB Base/Aftereffect)
Veridical Feedback
(FB Base/Washout)
Rotation
Probe
Target
Feedback
Rotated Feedback
45°
Early
Late
"Move the cursor to the target!"
"Move your hand to the target!"
B
No FB Base
FB Base
Learning 1
Rotation 1
Probe 1
Early
Late
No FB Aftereffect 1st
FB Washout
Learning 2
Rotation 2
Probe 2
No FB Aftereffect 2nd
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)
Hand Angle (deg)
F
Late learning
p=0.968
Individual difference (2 - 1)
Hand Angle (deg)
G
Early learning
p=0.015
Individual difference (2 - 1)
Hand Angle (deg)
H
Late learning
p=0.063
Individual difference (2 - 1)
Hand Angle (deg)
I
Aftereffect
p=0.002
Individual difference (2 - 1)
Hand Angle (deg)

Figure 2

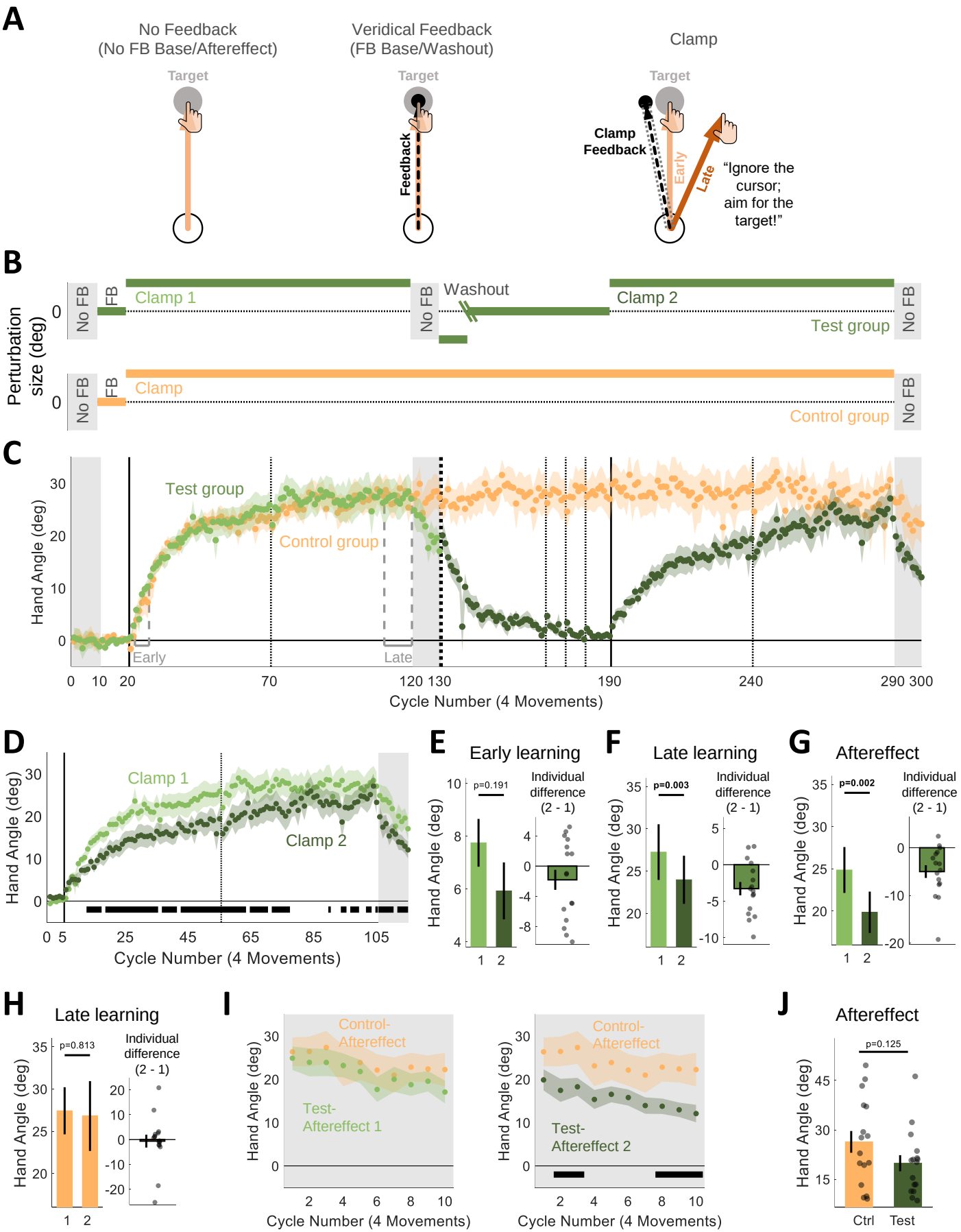
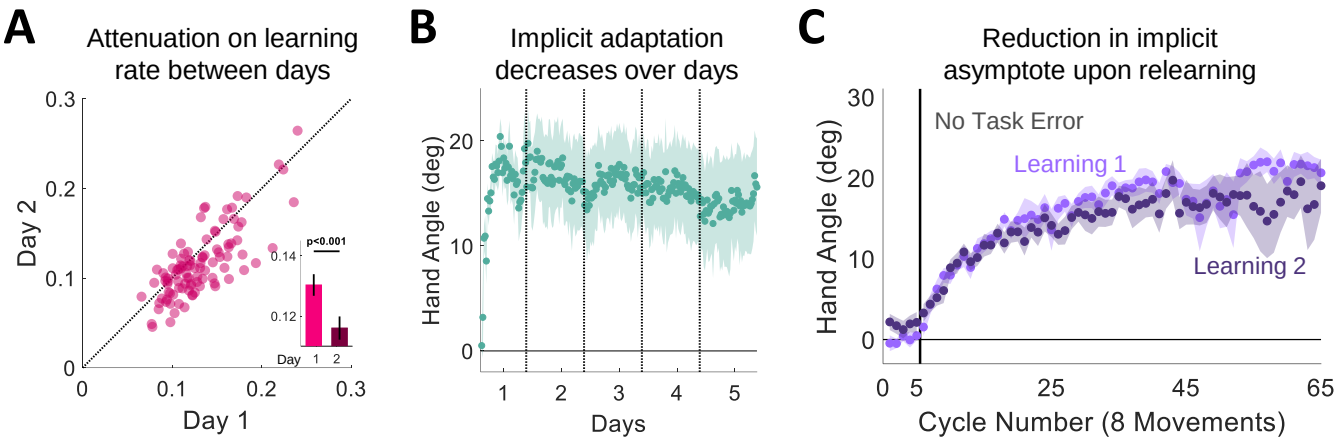

A
No Feedback
(No FB Base/Aftereffect)
Veridical Feedback
(FB Base/Washout)
Clamp
Target
Feedback
Clamp
Feedback
Early
Late
"Ignore the cursor; aim for the target!"
B
Perturbation size (deg)
No FB
FB
Clamp 1
Washout
Clamp 2
Test group
Clamp
Control group
C
Hand Angle (deg)
Test group
Control group
Early
Late
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
Control-Aftereffect
Test-Aftereffect 1
Test-Aftereffect 2
Cycle Number (4 Movements)
J
Aftereffect
p=0.125
Ctrl
Test

Figure 3


A
Attenuation on learning rate between days
Day 2
Day 1
0
0.1
0.2
0.3
p<0.001
0.14
0.12
Day 1 2
B
Implicit adaptation decreases over days
Hand Angle (deg)
Days
0
10
20
1
2
3
4
5
C
Reduction in implicit asymptote upon relearning
Hand Angle (deg)
Cycle Number (8 Movements)
No Task Error
Learning 1
Learning 2
0
10
20
30
0
5
25
45
65