Learning from Failure: Action Performance Errors Stimulate Intentional Strategies, Not Implicit Learning

Anushka Oza[1*], Adarsh Kumar[1,2*] and Pratik K. Mutha[1,3,#]

[1]Center for Cognitive and Brain Sciences, [2]Department of Mechanical Engineering, and [3]Department of Biological Engineering, Indian Institute of Technology Gandhinagar, Gujarat - 382355, India.

[*]Equal contribution
[#]Corresponding author

Contact Information:

Pratik K. Mutha
Block 5, Room 316A
Indian Institute of Technology Gandhinagar
Palaj, Gujarat 382355
India
Email: pm@iitgn.ac.in

ABSTRACT

Errors in task performance, such as the failure to strike a ball with a bat, are common in everyday actions. How do humans respond to such errors and the corresponding absence of rewarding outcomes? We test the hypothesis that action performance failures drive implicit refinements in motor plans. We employ a learning paradigm wherein we manipulate the location and size of a reach target while “clamping” visual feedback of the motion in a fixed direction, resulting in either performance failures or success. Our results fail to support the view that performance errors trigger implicit recalibration, and rather suggest that they set in motion a distinct, verbally-responsive, volitional strategy to select actions which rapidly reduce future errors. Our findings also indicate that for implicit learning to occur, exposure to sensory prediction errors is necessary. When prediction-error-driven implicit learning and performance-error-driven deliberative strategies combine, improvement in behavior is greater. However, when actions are always successful and strategies are not employed, performance gains are smaller. Flexibly employing cognitive strategies could thus be a way of controlling how much and how quickly we learn from errors.

INTRODUCTION

Humans must often perform actions under challenging conditions. For instance, a golfer may have to tee off against a constant breeze, or a dancer may have to perform while wearing a heavier-than-usual costume. Understanding how we adapt our actions to such changes and delineating the neural systems that support such learning has been of tremendous interest in cognitive neuroscience. Laboratory tasks often simulate such conditions using various visual (Kumar et al., 2020; Martin et al., 1996; Morehead et al., 2017) or dynamic (Sainburg et al., 1999; Shadmehr and Mussa-Ivaldi, 1994) perturbations. Such perturbing environments give rise to errors in our movements. For instance, they can create a mismatch between the intended and actual sensory consequences of action (sensory prediction errors) or result in a failure to accomplish the intended task goal (task performance errors). While it is well-recognized that we can learn to adjust our motor plans to account for the effects of such environments, the relative influence of various errors and the mechanisms they stimulate to enable such learning, are incompletely understood.

It is generally believed that sensory prediction errors drive iterative changes in motor plans by implicitly updating internal neural representations or models of the relationship between actions and their sensory consequences (Shadmehr et al., 2010; Wolpert and Flanagan, 2001). This is not very different from ideas in predictive coding theory, which emphasizes that the brain generates and updates internal models of the world in order to improve future expectations (Clark, 2013). There is extensive evidence that learning from prediction errors requires intact cerebellar and posterior parietal circuits. Cerebellar and parietal damage, or its disruption using artificial brain stimulation, impairs adaptation to visual (Kumar et al., 2020; Martin et al., 1996; Morehead et al., 2017; Mutha et al., 2011a) and dynamic (Della-Maggiore et al., 2004; Maschke et al., 2004) perturbations. Implicit learning driven by such errors has many interesting features: it evolves slowly (McDougle et al., 2015), asymptotes similarly for different error magnitudes(Kim et al., 2018; Wei and Körding, 2009), can be quite inflexible (Bond and Taylor, 2015) and is impervious to verbal instruction (Mazzoni and Krakauer, 2006; Morehead et al., 2017).

In contrast, controversy exists about how outcomes such as task success or failure influence updating of action plans. One possibility is that performance failures trigger intentional cognitive strategies to reduce perturbation-induced errors (Taylor et al., 2014). For example, failure to obtain reward upon missing a target may make people consciously aware of the perturbation and so they might deliberatively adjust their aim to compensate for that error. However, another view has emerged from recent work examining the influence of binary reward on error-based learning (Kim et al., 2019; Leow et al., 2018; Van der Kooij et al., 2018). These studies have shown that learning is greater when performance errors occur compared to when they do not; this effect can be explained by including a second, task-outcome-driven implicit process in a computational model of learning (Kim et al., 2019). Thus, in this framework, performance failures and the corresponding absence of reward can set in motion a second, independent implicit process that sums with prediction-error-mediated implicit learning to determine the net change in action plans. Given these dichotomous hypotheses – one positing deployment of volitional strategies and the other advocating for implicit updates – a clear understanding of the mechanistic effects of task outcomes, particularly performance failures, has remained elusive.

We set out to decisively test whether performance failures induce implicit updates to action plans. Our results suggest fail to support this hypothesis. They rather bolster the view that such failures trigger time-consuming strategic processes that are responsive to verbal instruction. Our findings further suggest that sustained task success reduces or eliminates strategy use during learning. Finally, we note that implicit learning is driven only by sensory prediction errors. We suggest that flexibly combining these two mechanisms could be a way for the sensorimotor system to optimize how much and how rapidly we learn from errors.

RESULTS

Experiment 1: Performance failures lead to greater changes in motor output

In our first experiment, participants performed targeted reaching movements in three blocks: baseline, learning and washout. The hand was not directly visible during the

reach, but visual feedback was provided by means of an on-screen cursor (Figure 1a). Participants were divided into two groups, “Hit” and “Miss”. Miss participants always experienced task performance failures, while the Hit participants always obtained task success (Figure 1b).

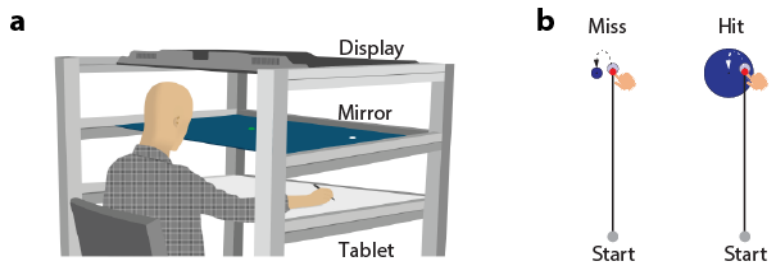

Figure 1. (a) *Subjects performed reaching movements on a digitizing tablet using a handheld stylus while looking into a mirror placed between the tablet and a horizontally mounted display screen. Start positions, targets, and a feedback cursor were displayed on the screen, which were reflected in the mirror.* ***(b)*** *On learning trials, the target was displaced, or “jumped” 10° counter-clockwise, while cursor motion was clamped in the direction of the original target. For the Miss group, this resulted in a performance failure since the cursor failed to strike the new target. For the Hit group, target size was increased along with the jump, which caused the clamped cursor to always hit the new target despite the shift in its location.*

When exposed to target shifts on learning trials, Hit participants began gradually aiming towards the (center of) the new target but did not go outside the target envelope (Figure 2a). Miss participants (Figure 2b) also began directing the hand to the new target, but remarkably, continued to aim well beyond it, with some saturation emerging towards the end of learning. This pattern was consistent across all subjects (Figure 2c). During early learning, hand deviation was not different between the Hit and Miss participants (Figure 2d; Hit: 0.910±0.630°, Miss: 3.870±1.727°, $t(17.66) = -1.61$, $p = 0.125$, Cohen’s $d = -0.588$), although on average the deviation of the Miss group had already increased from zero (mean = 3.870±1.727, CI = [0.166, 7.573]). The Miss group also showed a larger change in reaction time (RT) from late baseline levels compared to the Hit group (Figure 2e; $t(18.94) = -3.07$, $p = 0.0063$, Cohen’s $d = -1.123$). In fact, RT for Hit participants was not different from baseline ($t(14) = 0.25$, $p = 0.806$, Cohen’s $d = -0.065$).

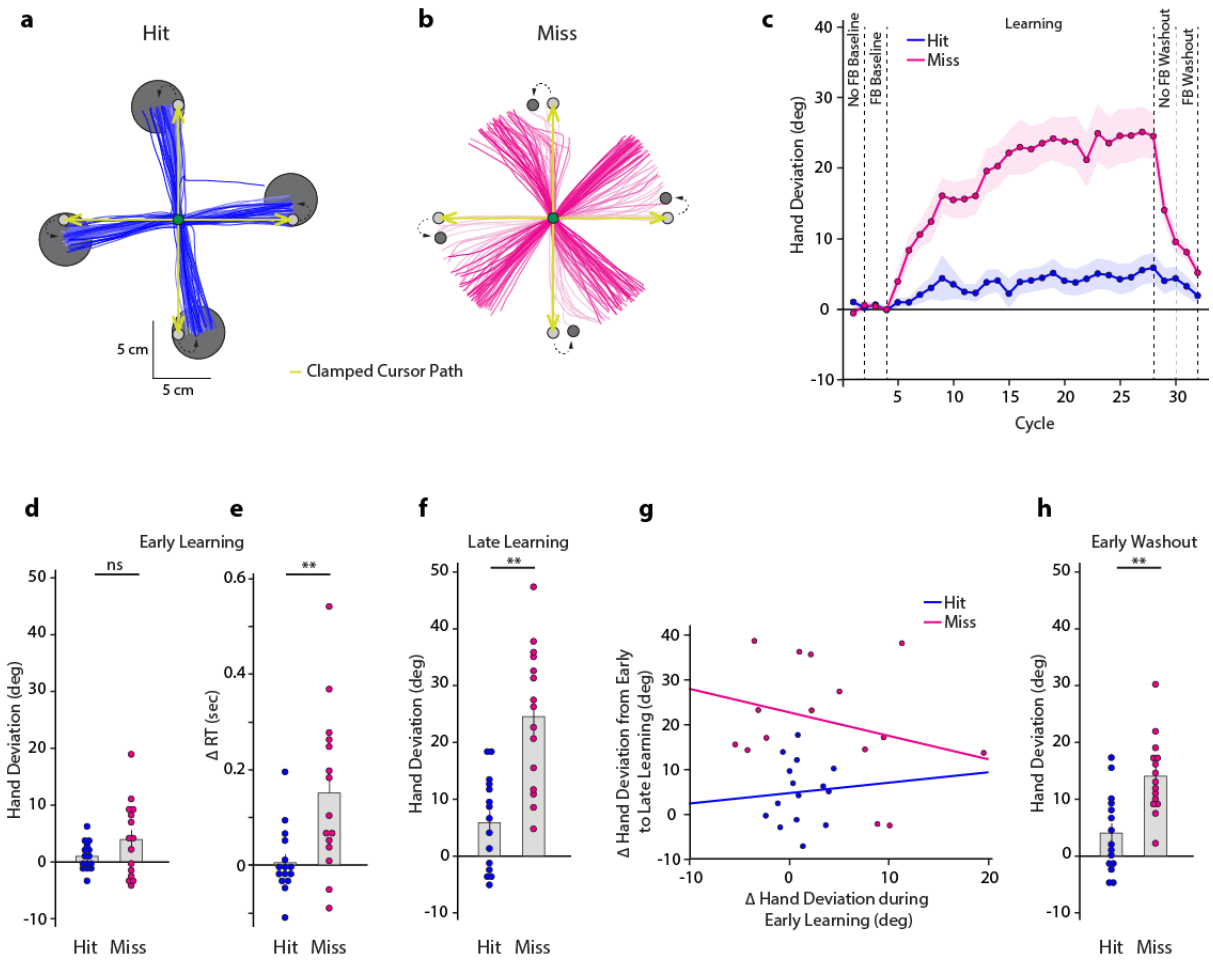

Figure 2. *Hand trajectories of example subjects of the* ***(a)*** *Hit and* ***(b)*** *Miss groups during the learning block. Earlier trials are in lighter shades. The first 10 cm of the movement (corresponding to the target distance) are shown. The cursor path is indicated by green arrows.* ***(c)*** *Group averaged hand deviation (relative to the original target direction) across cycles of the experimental blocks. Shaded regions denote SEM.* ***(d)*** *Hand deviation and* ***(e)*** *change in RT during the early learning phase.* ***(f)*** *Hand deviation during late learning. Dots represent individual participants.* ***(g)*** *Relationship between the change in hand deviation from baseline to early learning, and the change in hand deviation over the rest of the learning block.* ***(h)*** *Hand deviation during the early no-feedback washout phase.*

As learning progressed, changes in reach direction occurred in both groups. However, by the end of learning, the Miss group had deviated much more (Figure 2f, $t(23.99) = -4.878$, $p < 0.001$, Cohen's $d = -1.781$). Critically, it was not the case that the Hit group showed no change; a direct comparison between the early and late learning phases of this group revealed a clear increase in hand deviation ($t(14) = -2.726$, $p = 0.016$, Cohen's $d = -0.704$). However, relative to Miss participants, this learning was conspicuously attenuated. Interestingly though, we found no

relationship between the change in hand angle from late baseline to early learning, and the change over the remainder of the learning block (Figure 2g; Hit: $R^2 = 0.004$, $p = 0.812$; Miss: $R^2 = 0.082$, $p = 0.3$). The absence of such an association suggested that changes in hand angle beyond the initial stage were largely independent of changes that might have occurred early on (also see Supplementary Information).

During early washout (without cursor feedback), hand deviation continued to be large for the Miss group (13.978±1.740°), indicating the presence of after-effects. After-effects were also evident in the Hit group (3.960±1.792°, CI = [0.117, 7.803]) although they were smaller (Figure 2h; $t(27.98) = -4.011$, $p < 0.001$, Cohen's d = -1.465). Importantly, these after-effects were sustained for an extended period, with both groups continuing to show large deviations even after cursor feedback was restored (Miss: 8.026±0.966°, CI = [5.955, 10.097]; Hit: 3.191±1.442°, CI = [0.1, 6.283]). In fact, for the Miss group, after-effects did not return to zero even after all washout trials had ended (mean = 5.114±1.036°, CI = [2.891, 7.336]). This persistence of after-effects in both groups suggested that their change in reach direction had occurred implicitly. This was supported by two more observations: first, learning occurred despite the instruction to ignore cursor feedback (see Methods), and second, the net change in hand angle was much larger than the error magnitude in the Miss group. Both effects are known to occur when the updating of action plans proceeds implicitly(Kim et al., 2019; Ryan Morehead et al., 2017).

Mathematical modeling

What drives this implicit learning? To address this question, we considered variants of the single-rate state space learning model, which has the following general form:

$$x(n+1) = A*x(n) + B*e(n) \quad (1)$$

Here *e* represents the error on the nth trial, *x* represents an internal state, and *A* and *B* represent a retention factor and error sensitivity respectively.

We first explored an architecture in which implicit learning is driven only by performance failures. Therefore, e(n) in the above equation was replaced by a constant task performance error (TPE), and model equations were modified as:

$$x_{TPE}(n+1) = A_{TPE} * x_{TPE}(n) + B_{TPE} * TPE \quad (2)$$

In this model, state updates occurred only in the Miss condition since performance errors were absent on Hit trials (these subjects were always successful). This model thus predicted no learning in the Hit group but a change in motor output for the Miss participants (Figure 3a). However, this deviated from the observations of experiment 1 in which *both* groups showed a change in hand angle as well as post-learning after-effects.

We then considered an alternate possibility that the observed implicit learning was mediated solely by a sensory prediction error (SPE) that got created as the Hit and Miss subjects began to reach directly towards the new target while cursor motion continued to be clamped towards the original target. In this model, the performance error had no influence. The model equations were modified as:

$$x_{SPE}(n+1) = A_{SPE} * x_{SPE}(n) + B_{SPE} * SPE \quad (3)$$

This model was similar to that of equation (2), except that the task performance error was replaced with a sensory prediction error. Importantly, the prediction error was always present, and its magnitude was the same (10-degrees), for the Hit and Miss participants. Hence, this model predicted similar learning curves for both groups (Figure 3b). However, this was again not in harmony with the experimentally observed attenuated learning of the Hit participants.

Since the first two models failed to predict the experimentally observed pattern, we evaluated a third model in which state updates were driven by a combination of two independent implicit processes, one sensitive to prediction errors (equation 5) and the other to performance errors (equation 6).

$$x(n) = x_{SPE}(n) + x_{TPE}(n) \quad (4)$$

$$x_{SPE}(n+1)=A_{SPE}*x_{SPE}(n)+B_{SPE}*SPE \quad (5)$$

$$x_{TPE}(n+1)=A_{TPE}*x_{TPE}(n)+B_{TPE}*TPE \quad (6)$$

The key aspect of this model is how the states were updated for the Hit and Miss groups. Since both groups experienced prediction errors, this term (equation 5) was updated for both groups. However, since the Hit group did not experience any performance errors, the corresponding term (equation 6) was updated only for the Miss participants. This model thus predicted group differences in motor output (Figure 3c).

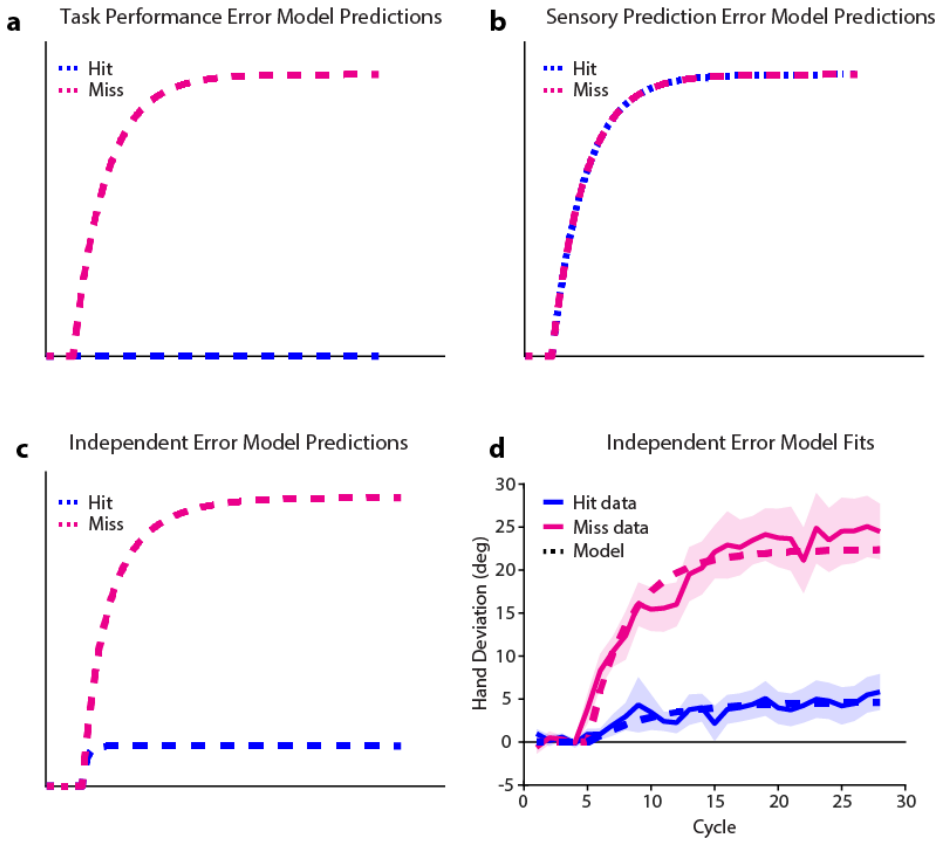

Figure 3. (a) *Simulated hand deviation derived from a model wherein implicit learning is driven only by task performance errors (TPE). This model predicts no change in hand angle (no learning) for the Hit group since a TPE is absent, but predicts asymptotic learning for Miss participants.* ***(b)*** *Predictions of a model in which only a sensory prediction error (SPE) drives implicit learning. This model predicts similar changes in hand deviation for the Hit and Miss groups since the SPE is the same in both cases.* ***(c)*** *Predictions of an independent error model in which both SPE and TPE trigger distinct implicit processes, and net learning is their summed output. This model predicts greater learning for*

the Miss group since this group experiences both types of errors while only the SPE is present in the Hit group. ***(d)*** *Independent error model fits to the data of experiment 1. Solid lines represent the experimentally observed hand deviation while dashed lines represent the model fits. Shaded region denotes SEM. The model was first fit to data of the Hit group (R^2 = 0.81, RMSE = 0.7553) to estimate A_{SPE} and B_{SPE}*SPE. The parameter values obtained were 0.8184 and 0.8441 respectively. These values were then used when fitting the model to data of the Miss group (R^2 = 0.90, RMSE = 2.6833), and A_{TPE} and B_{TPE}*TPE were estimated as 0.7987 and 3.9622 respectively.*

Since the Hit participants did not experience performance errors, we first fit only the prediction-error-based component to the Hit participants' data (Figure 3d, blue dashed line) and estimated the A_{SPE} and B_{SPE}*SPE values. We then used these estimates when fitting the combined model to the data of Miss participants (Figure 3d, pink dashed line), and estimated A_{TPE} and B_{TPE}*TPE. We found that B_{TPE}*TPE was 4.7 times greater than B_{SPE}*SPE, suggesting that the performance-error-sensitive process "pulled up" the learning curve when failures occurred, ultimately resulting in differences between the Hit and Miss groups.

Experiment 2: Performance failures can be ignored when instructed

The success of this model suggested that it was at least *mathematically* possible to account for the greater learning in the Miss group via an implicit mechanism triggered by performance errors that acts in concert with another prediction-error-driven implicit process. A pivotal *empirical* prediction of this framework however is that such learning should occur even when participants are explicitly told to ignore the shift in target location; this is because implicit learning is impervious to verbal instruction (Mazzoni and Krakauer, 2006b; Morehead et al., 2017). We tested this hypothesis in our second experiment. We recruited two groups pf participants that underwent learning like the Miss group of experiment 1, but were told to ignore the (10° or 20°) jump and reach to the original target location.

Surprisingly, we now found no change in reach direction. As can be seen in Figures 4a and 4b, the hand was almost always directed towards the original target, even though it had been extinguished and a new one was displayed at a location 10° (Figure 4a) or 20° (Figure 4b) clockwise from it. The absence of a change in reach direction was consistent in the group-averaged data as well (Figure 4c). During early

learning, hand deviation (Figure 4d) remained close to zero for the 10° (-0.154±0.29°, CI = [-0.777, 0.468]) as well as the 20° (0.687±0.378°, CI = [-0.123, 1.498]) groups. This continued to be the case at the end of learning as well (Figure 4d; 10°: -1.843±0.887°, CI = [-3.747, 0.06], 20°: -1.182±0.863°, CI = [-3.033, 0.67]). Relatedly, after-effects on the early no-feedback washout trials were also absent in both groups (Figure 4d; 10°: -0.951±1.183°, CI = [-3.488, 1.585]; 20°: -0.648±0.708°, CI = [-2.167, 0.871]). This continued to be the case in the second washout block in which visual feedback was restored (10°: -1.051±0.702°, CI = [-2.556, 0.453]; 20°: = -0.033±0.612°, CI = [-1.345, 1.278]).

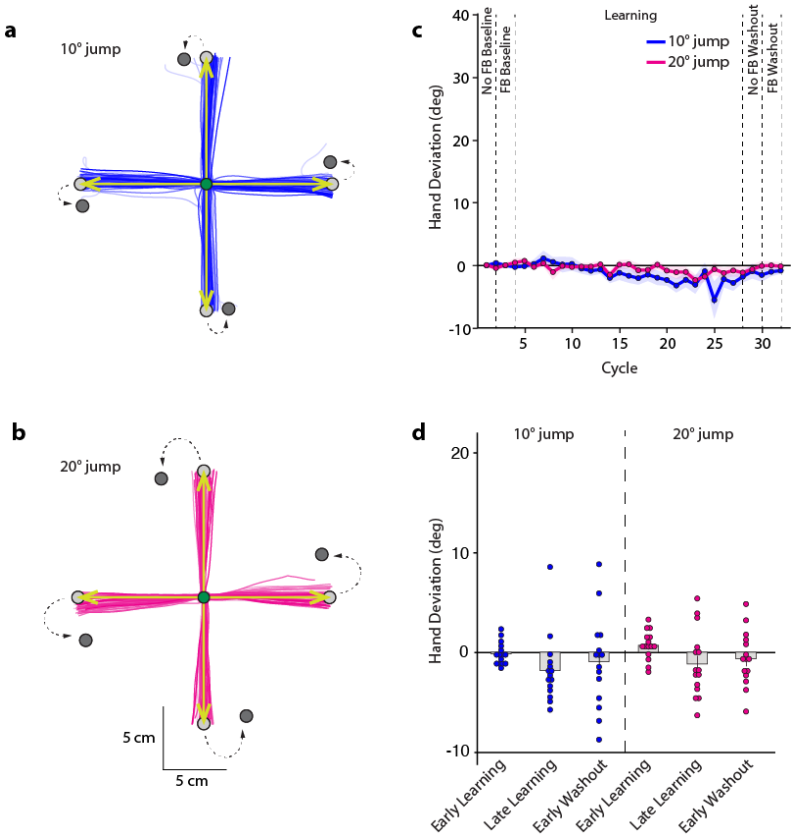

Figure 4. *Hand trajectories of example subjects in the 10° **(a)** and 20° **(b)** target displacement groups during the learning block. Earlier trials are in lighter shades. The first 10 cm of the movement are shown. The green arrows indicate the clamped cursor trajectory. **(c)** Group-averaged hand angle deviation across cycles of different blocks. Shaded regions denote SEM. **(d)** Mean hand deviation during the early and late learning stages, as well as the early washout phase. Dots represent individual subjects.*

Thus, when instructed to ignore performance failures, no adaptive changes in reach behavior occurred; this would *not* be the case if these errors were driving implicit changes in reach plans. This also meant that implicit recalibration in experiment 1 was set off solely by a sensory prediction error, but the net change in behavior was influenced by a different, verbally-responsive mechanism engaged when performance failures occurred.

Experiment 3: Performance failures trigger deliberative strategies

What form does this instruction-sensitive mechanism that responds to performance error take? In our third experiment, we tested the hypothesis that performance failures set in motion a deliberate, volitional strategy of aiming the hand away from the original target and towards the new one. We exposed participants to performance errors via a 10° target shift that resulted in performance errors. Additionally, the feedback cursor motion was made congruent with the hand, i.e. it was no longer clamped, thereby eliminating sensory prediction errors. We predicted that subjects would show increased RT and fleeting after-effects, classic signatures of a re-aiming strategy (Fernandez-Ruiz et al., 2011; McDougle and Taylor, 2019; Neville and Cressman, 2018).

Figure 5a shows the hand trajectories of an example subject from this experiment. As is evident, the hand was directed towards the displaced target within a few trials, but did not go substantially beyond it. This was true for the group as a whole, as evidenced by the asymptote in the mean hand deviation following an increase in the first few learning cycles (Figure 5b). We observed a robust change in hand angle (relative to late baseline) during the early learning stage itself (Figure 5c; $t(9) = 3.76$, $p = 0.0045$, Cohen's $d = 1.189$). This suggested that participants tried to account for the (predictably) changing target location quite rapidly. Notably, there was also an increase in RT (Figure 5d) during the early learning phase by ~100 ms (mean±SE = 96.17±24 ms), a change that was clearly statistically significant ($t(9) = 4.015$, $p = 0.003$, Cohen's $d = -1.27$). By the end of the learning block, the mean change in hand angle from the late baseline stage was 9.014±0.653 degrees, which was remarkably close to the magnitude of the target jump (Figure 5c). Furthermore, in

sharp contrast to the Hit and Miss groups of experiment 1, early changes in hand angle were negatively correlated with changes over the rest of the learning block (Figure 5e; $R^2 = 0.587$, $p = 0.0097$). Thus, if the initial change in hand angle was large enough to offset the error, no further learning occurred (Supplementary Information).

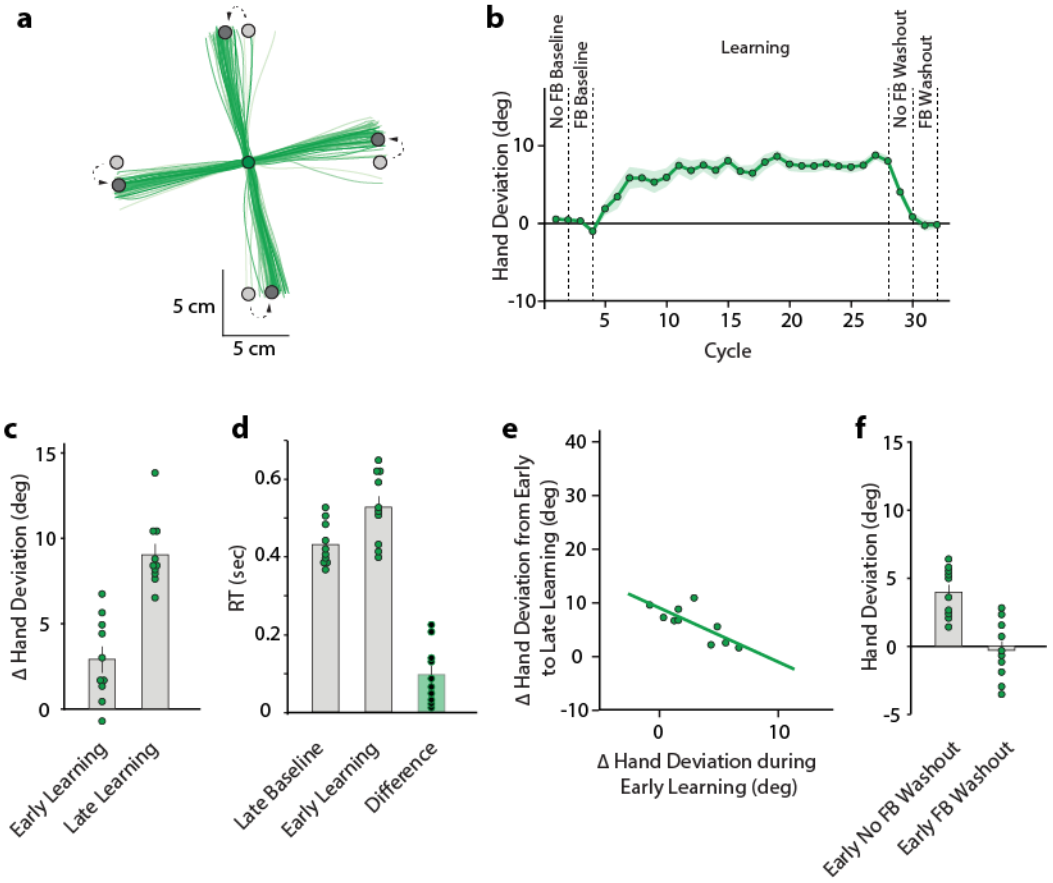

Figure 5. (a) *Hand trajectories of an example subject during the learning block. Earlier trials are in lighter shades. The first 10 cm of the movement are shown.* ***(b)*** *Group averaged hand deviation across cycles of different experimental blocks. Shaded regions denote SEM.* ***(c)*** *Change in hand angle during early and late learning relative to the late baseline stage. Dots are individual participants* ***(d)*** *Group-averaged RT during the late baseline and early learning phases.* ***(e)*** *Negative correlation between change in hand angle from baseline to early learning, and change in hand angle thereafter.* ***(f)*** *Group-averaged hand deviation on the early no-feedback and feedback washout trials.*

On washout trials (Figure 5f), the hand was somewhat deviated early on (mean = 3.95±0.566°, CI = [2.667, 5.227]), but this was not sustained, and performance rapidly decayed towards baseline. By the end of the first washout block, the deviation was already near zero (mean = 0.757±0.526°, CI = [-0.434, 1.948]). This

continued to be the case on the early (mean = -0.33±0.683°, CI = [-1.875, 1.216]) and late (mean = -0.245±0.452°, CI = [-1.266, 0.777]) feedback washout trials. Additional analyses involving a direct comparison of this decay to that of the Hit and Miss groups of experiment 1, confirmed the highly labile nature of the after-effects (Supplementary Information). This result, complemented with the early increase in RT on learning trials, indicated that subjects changed their reach direction primarily by employing time-consuming re-aiming strategies that were rapidly disengaged when no longer relevant.

DISCUSSION

We probed how task outcomes in the form of failure or success in achieving task goals influence adaptive changes in motor output. Collectively, our results challenge the notion that performance failures trigger implicit recalibration of action plans. Rather, our results indicate that implicit learning is engaged only by sensory prediction errors. In the first experiment, this prediction error gets created as subjects begin to change their reach direction towards the new target (and expect the cursor to go with it) while actual cursor motion remains clamped towards the original target. This is just like a “classical” sensory prediction error that occurs as people move in an instructed direction while feedback of that motion is shown in another; such prediction errors are known to trigger implicit learning. In experiment 2, the hand (as instructed to subjects) and the cursor (as controlled by the experimenter) are both directed towards the original target, thus eliminating the prediction error and causing no adaptive response even though performance errors are present.

These findings are reminiscent of classic work that demonstrated that in the presence of prediction errors, humans compulsively update their action plan in an implicit manner even if such learning bears a cost on performance errors (Mazzoni and Krakauer, 2006). Relatedly, stroke patients with lesions to right inferior frontal and dorsolateral prefrontal cortices, who demonstrate clear performance failures when exposed to a perturbation, have no problem implicitly updating their reach direction (Mutha et al., 2011b). These past results, and also the current work, are

aligned with suggestions of predictive coding theory which proposes that the brain always strives to eliminate sensory prediction errors by updating an internal model to improve future predictions (Clark, 2013). Tellingly, recent work (Wang et al., 2019) suggests that the prediction error dominance may be so strong that task outcomes may have negligible influence, at least in canonical learning paradigms. Our results also strengthen this view.

If implicit learning is driven by sensory prediction errors, how do task outcomes contribute? One possibility is that performance failures “modulate” prediction-error-driven implicit learning (Kim et al., 2019). A mathematical formulation of this possibility (Supplementary Information) can indeed account for the data of experiment 1. However, such a framework implies that this influence is directly on the error sensitivity or retention of the implicit process. Our data rather supports an alternate view – that performance failures set in motion a *distinct*, intentional mechanism that causes people to re-aim their hand movement (Taylor et al., 2014). Thus, when people are expected to respond to a performance error, they deliberatively change their aim to cancel it; this leads to a more rapid change in reach direction early on. Likewise, when asked to ignore performance errors, people can simply “turn off” the use of this strategy. Pertinently, aiming strategies might also be disengaged when actions are always successful or rewarded. Such flexibility is indeed a hallmark of strategy use (Bond and Taylor, 2015). In the absence strategy use, net updates to action plans would be determined only by the implicit process. This is different from direct modulation of implicit learning itself, and can explain not just the attenuated learning in Hit participants, but also results of other recent studies in which performance errors were eliminated (Kim et al., 2019; Leow et al., 2018; Van der Kooij et al., 2018). Complementarily, incomplete learning could be made more complete by promoting strategy use (Langsdorf et al., 2021). While the specific nature of these strategies remains to be uncovered, potential candidates include mental rotation of the original movement plan (Fernandez-Ruiz et al., 2011; McDougle and Taylor, 2019) or time-consuming, goal-directed control.

Notably, beyond compensating for performance failures, strategy use could act as a gateway to long-term storage of updates made to actions plans and expression of the acquired memory as savings. In particular, strategies that lead to rewarding task

outcomes could be reinforced and recalled later, resulting in faster learning upon re-exposure to the original learning conditions (Huberdeau et al., 2015; Morehead et al., 2015). On the other hand, conditions where strategy formation is prohibited by limiting movement planning time, preventing exposure to performance errors or forcing only implicit learning, might block savings (Haith et al., 2015; Leow et al., 2020). This suggests that unsuccessful task outcomes and associated strategy use are essential for forming long-term motor memories.

The distinction between processes that prediction errors and performance errors trigger suggests that these mechanisms could be neurally separable. While prediction-error-based implicit learning depends on the cerebellum (Martin et al., 1996; Morehead et al., 2017) and parietal cortex (Della-Maggiore et al., 2004; Kumar et al., 2020; Mutha et al., 2017), performance failures activate reward-sensitive cortico-striatal pathways (Diedrichsen et al., 2005; Inoue et al., 2016). Failure to obtain reward could trigger re-aiming via processes dependent on M1 and premotor cortex (Georgopoulos et al., 1989; Kosslyn et al., 1998). Changes in these regions following learning (Paz et al., 2003; Perich et al., 2018) may thus partially reflect changes in action plans driven by such processes. Future work could probe the communication between these two systems, which, neuroanatomically, could be sustained by reciprocal connections between the basal ganglia and the cerebellum (Bostan and Strick, 2018).

MATERIALS AND METHODS

Participants

We recruited 70 healthy, right-handed adults (47 males, 23 females, age range: 18-40) for the study. None of the participants reported any neurological, orthopaedic or cognitive impairments. All subjects gave written informed consent and were monetarily compensated for their time. The project was approved by the Institute Ethics Committee of the Indian Institute of Technology Gandhinagar.

Apparatus

The experimental setup consisted of a virtual reality system wherein participants sat facing a digitizing tablet and used a stylus to make hand movements on it (Figure 1a). A high-definition display was mounted horizontally above the tablet and was used to show circular start positions and targets for the reach, as well as a feedback cursor that would typically indicate hand (stylus) location on the tablet. Participants looked into a mirror which was placed between the display and the tablet, and which reflected the display screen. The mirror also functioned to block direct vision of the arm. This arrangement enabled us to dissociate motion of the feedback cursor from that of the hand. For instance, cursor feedback could be veridical with the hand, “clamped” in certain directions independent of hand movement direction, or eliminated altogether.

Task Procedure and Experimental Design

The task involved making centre-out reaching movements from a fixed start circle (0.9 cm diameter) to a target. To initiate a trial, participants first moved their hand (cursor) into the start circle. After 500 ms, the reach target (0.98 cm diameter) was displayed along with a beep, which indicated to subjects that they should begin moving. No constraint was placed on reaction time or movement time. Targets were presented at a distance of 10 cm and could appear at one of four locations arranged radially around a virtual circle in 90-degree increments (0°, 90°, 180°, 270°). The order of target appearance was pseudo-random; a target appeared in one of the four locations only once over four consecutive trials. This order was maintained across all participants. Cursor feedback, whenever provided, was shown continuously (throughout the movement) for a distance of 10 cm at which point the cursor “froze” and stayed in place even though the hand could continue moving.

In all our experiments, after familiarization with the setup and a few practice movements (not analyzed), subjects performed 3 continuous blocks of trials: baseline, learning and washout. The baseline and washout blocks comprised of two sub-blocks each. In the first baseline sub-block (20 trials), the feedback cursor was

not shown during the reach, while in the second (20 trials), the cursor was shown veridical with the hand. Following baseline, subjects experienced 240 learning trials (see below for details), which were followed by the two washout sub-blocks that were identical to baseline (20 no feedback trials, 20 veridical feedback trials). Each subject thus performed 320 experimental trials in all. During the baseline and washout blocks, the originally displayed target (at one of the 0°, 90°, 180°, 270° locations) remained "stationary", i.e. its location did not change during the trial. During the learning block however, the target was displaced, or "jumped", by 10° in the counter-clockwise direction on every trial. This was achieved by extinguishing the originally presented target as the hand reached mid-way to it, and displaying a new target at the 10°, 100°, 190° or 280° locations. Importantly, in experiments 1 and 2, the motion of the feedback cursor on these learning trials was always "clamped" in the direction of the original target. In other words, the cursor always followed a direct, straight path to the original target regardless of the direction of hand motion. The clamp was not used in experiment 3, and cursor motion remained congruent with that of the hand.

Subjects were explained the task conditions prior to start of the experiment. They were instructed to reach towards the target on the screen. For baseline and washout trials, this obviously meant the original, fixed target. However, for learning trials, since the original target was extinguished and a new one displayed on the screen in an easily-predictable location (always 10° counterclockwise to the original target), subjects could start aiming directly in the direction of the new target. No attempt was made to either dissuade or encourage this behavior.

Experiment 1

The participants of experiment 1 were randomly divided into two groups, "Miss" or "Hit" (n=15 each) that differed in terms of the learning trials. For the Miss group, the original and the new target were of the same size (0.98 cm diameter), but for the Hit group, the diameter of the new target was increased from the original 0.98 cm to 4.6 cm (Figure 1b). Since cursor motion was clamped towards the original target, the target jump resulted in the cursor missing the new target, creating a task

performance failure for the Miss group. However, for the Hit participants, the increase in target size ensured that the cursor would still hit the new target, thus preventing the task error. This hit was obviously not in the center of the new target. In addition to being told to reach towards the on-screen target, subjects were also informed and made to understand that on the jump trials, cursor motion would be fixed and would not depend on the direction of their hand movements. They were also explicitly told to ignore this cursor feedback. A reminder to this effect was provided at the halfway point of the learning block.

Experiment 2

In experiment 2, we recruited two additional groups of subjects (n=15 each), who experienced target jumps of two different amplitudes (10° or 20°) while the cursor remained clamped in the direction of the original target. This led to conditions similar to the Miss group of experiment 1 where the cursor did not strike the new, shifted target thus creating task errors. Critically however, both groups of subjects were now also explicitly instructed to ignore the change in target location and reach towards the original location. As in experiment 1, subjects were reminded of this halfway into the learning block.

Experiment 3

In our third experiment (n=10), subjects once again experienced target jumps like the Miss group of experiment 1 (no increase in target size), but the feedback cursor was no longer clamped during learning trials. Rather, cursor motion was always veridical with hand motion. Other aspects including instructions remained the same as experiment 1.

Mathematical modelling

Experiment 1 revealed that subjects in the Hit and Miss groups underwent implicit learning. To probe its underlying basis, we considered different forms of a single-rate

state-space model of motor adaptation (Kim et al., 2019). The model equations are typically of the following form:

$$x(n+1) = A*x(n) + B*e(n)$$

where *e* represents the error on the nth trial, *x* represents the motor output, and *A* and *B* represent a retention factor and error sensitivity respectively.

Performance error model

In our first variant of the above model, we considered that learning is driven only by the task performance error (TPE). Therefore, the e(n) term was replaced by the TPE term:

$$x(n+1) = A_{TPE}*x(n) + B_{TPE}*TPE$$

Since the TPE is absent on Hit trials, state updates do not occur in this condition. This model therefore predicts no change in motor output (hand angle) in the Hit condition. However, this deviated from the experimentally observed data wherein the Hit group showed clear changes in hand angle.

Sensory prediction error model

Since the performance error driven model could not account for the behavioral findings, we considered another variant in which a sensory prediction error (SPE) error drives learning and the performance error has no influence. In this model, the error term getss replaced by the SPE, corresponding to the mismatch between the subjects intended reach direction (towards the new target) and clamped cursor motion towards the original target. The model equations are:

$$x(n+1) = A_{SPE}*x(n) + B_{SPE}*SPE$$

Because of the clamp, the SPE magnitude remains fixed for both groups. This model thus predicts the same change in hand angle for the Hit and Miss participants. Our behavioral data however showed clearly attenuated changes for the Hit compared to the Miss group. This model was thus also inadequate in terms of being able to predict behavioral results.

Independent error model

Next, we considered a framework in which both sensory prediction errors (SPE) and performance errors (TPE) drive independent implicit processes. The net motor output reflects the sum of these SPE- and TPE-based processes. The model equations are:

$$x(n) = x_{SPE}(n) + x_{TPE}(n)$$
$$x_{SPE}(n+1) = A_{SPE} * x_{SPE}(n) + B_{SPE} * SPE$$
$$x_{TPE}(n+1) = A_{TPE} * x_{TPE}(n) + B_{TPE} * TPE$$

In the Hit condition, the TPE-based update does not occur (since TPE = 0) and learning can be presumed to be driven only by the SPE-based process. However, for the Miss case, both processes get updated since the SPE and TPE are both present, and the net output is the sum of these two processes. This model is able to predict reduced learning in the Hit compared to the Miss group.

We first fit only the SPE-sensitive process to the cycle-wise data of the Hit group using the *fmincon* function of Matlab. While fitting, B_{SPE}*SPE was estimated as a single parameter since the SPE remained fixed due to the clamp. A_{SPE} was the other parameter estimated from the fit. Data from the baseline, learning and no-feedback washout blocks were included, with the B_{SPE}*SPE term being set to zero for the no-feedback washout cycles. The feedback washout data were not used since the SPE was no longer constant in this condition (clamp was removed) and could change as subjects changed their hand direction. The estimated values of A_{SPE} and B_{SPE}*SPE derived from model fits to the Hit participants' data were then used while fitting the model (including the TPE-based process) to the data of the Miss participants. Thus, only A_{TPE} and B_{TPE}*TPE terms were estimated from these latter fits. For both fits,

A_{SPE} and A_{TPE} were constrained between 0 and 1, while B_{SPE}*SPE and B_{TPE}*TPE were constrained between 0 and 10°. The 10° value corresponds to the maximum "error" (angle between new target direction and clamped cursor direction) on any given trial.

Empirical Data Analysis and Statistics

Hand position data (X-Y coordinates) were filtered using a low-pass Butterworth filter with 10-Hz cutoff frequency. Velocity values were obtained by differentiating the position data. The primary dependent variable was the deviation in hand direction relative to the original target direction. This was computed as the angle between the line connecting the start position to the original target, and the line connecting the start position to the hand position at peak movement velocity. Trials in which participants did not initiate a movement or lifted the stylus off the tablet mid-trial leading to loss of data were marked as "bad trials" and excluded from the analysis. Additionally, trials in which hand deviation was more than 85˚ were also removed. Collectively, across the 70 participants, 1.91% of the trials were excluded. We then calculated baseline directional biases, defined as the mean hand deviation across all baseline trials. These biases were subtracted from the trial-wise hand deviation data.

Learning was quantified using the cycle-by-cycle values of the baseline subtracted hand deviation over the learning block (1 cycle = 10 trials). For each subject, early learning was defined as the mean deviation over the first 10 learning trials while late learning was characterized by the mean deviation over the last 10 learning trials. Reaction time (RT) during early learning was assessed in terms of a change from late baseline levels. This was done by subtracting the mean RT of the last 10 baseline trials from the mean RT of the first 10 learning trials. Early after-effect magnitude was quantified as the mean deviation over the first 10 trials of the no-feedback washout block. To assess whether after-effects were sustained, their average magnitude on the first 10 trials of the feedback washout block was also calculated for each subject.

Group differences in hand deviation during early and late learning as well as the different after-effect stages were compared using Welch's t-tests after checking for normality with Shapiro-Wilk tests. Paired t-tests were used for assessing changes in hand deviation across different time points within a group. Significance levels were set at 0.05. Cohen's *d* was used for estimating the effect size of the differences. We also used the 95% confidence interval to probe for significant deviation in hand angle during early and late learning as well as the different after-effect stages.

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AUTHOR CONTRIBUTIONS

AO, AK and PKM designed the experiments. AO collected the data, all the authors analyzed the data and interpreted the results. All authors also wrote and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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SUPPLEMENTARY INFORMATION

1. Relationship between early and late changes in hand angle.

The Miss group of experiment 1 experienced performance failures. During the early learning stage, these subjects demonstrated larger RTs and increased hand deviation (relative to baseline). As our experiment 3 and other work[1,2] shows, such changes reflect the deployment of strategic processes that cause the hand to aim away from the original target. Importantly however, this early strategy use had no bearing on how their hand angle changed over the remainder of the learning block; there was no relationship between the change in hand angle during early learning and the change thereafter until the end of learning (Figure 1h of main manuscript). Our data suggest that the latter changes are driven by unconscious, implicit mechanisms which are engaged as subjects intend to aim to the new target location while cursor motion is clamped in the direction of the original target. Put together, our data for the Miss group suggests that the intent to aim to the new target likely emerged via explicit re-aiming with implicit mechanisms taking over thereafter.

The relationship between the early and later changes in hand deviation was also absent in the Hit group (Figure 1h of main manuscript). While on the face of it, this seems similar to the Miss group, the underlying reason is likely to be different. The Hit participants did not experience performance failures, and did not show any substantial change in hand angle or RT during the early learning stage. This suggests that unlike the Miss group, these participants did not employ deliberative mechanisms to change their aim towards the new target early on. Thus, the changes that emerged over the course of the learning block were driven entirely by an implicit process that was engaged as they gradually started aiming to the center of the new target while the cursor remained clamped in the original target. Thus, the absence of a relationship in the Hit group was because a single process was engaged. In contrast, for the Miss participants, the absence of a relationship was because two independent processes were engaged during the early and later learning phases.

Finally, the subjects of experiment 3 demonstrated a strong negative relationship between the early change in hand angle and subsequent changes (Figure 4e of main manuscript). This is interesting and indicates that if the early process “siphoned off” a large chunk of the error, no further changes in hand angle occurred. We suggested, based on the consistent increase in RT and hand angle during early learning as well as the very labile after-effects, that this process was a conscious, re-aiming strategy. Since the performance error was compensated via this mechanism, and a prediction error was not present, an additional (implicit) learning mechanism was not engaged in this group.

2. Direct comparison of after-effects in experiments 1 and 3.

The Hit and Miss groups of experiment 1 showed sustained post-learning after-effects. Subjects of experiment 3, who experienced only performance errors, showed deviations in hand angle immediately after the learning block had ended, but this effect were not sustained. However, a direct comparison between these groups was precluded since the asymptotic level of learning was different between them. To overcome this issue, we used the following approach. We considered only the hand angle data of the last learning cycle and the four washout cycles (two no feedback, two feedback washout cycles). We then scaled the data of individual Hit participants of experiment 1 and the subjects of experiment 3 to match the mean hand angle of the Miss group on the last learning cycle. Thus, at the end of this step, the mean hand angle at the end of learning for all three groups was identical. We then compared the (scaled) after-effects across the three groups (Figure S1).

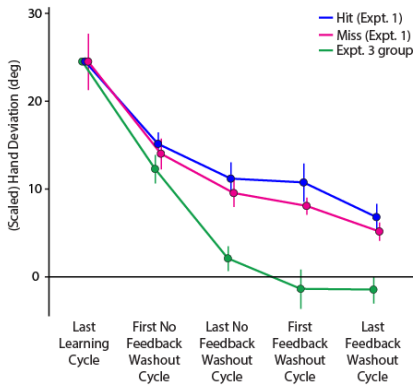

Figure S1: Direct comparison of after-effects in experiment 1 and experiment 3. *Scaled average hand deviation of the Hit and Miss groups of experiment 1 and the subject group of experiment 3. Data on the last learning cycle, the two no-feedback washout cycles and the two feedback washout cycles are shown. Error bars represent SEM. The (scaled) hand deviation on washout trials decayed more rapidly towards zero for the subjects of experiment 3.*

We found that hand deviation on the first no-feedback washout cycle was not different between the groups ($F(2,37) = 0.726$, $p = 0.491$, $\eta^2_p = 0.038$). However, on later no-feedback washout trials, clear group differences emerged ($F(2,37) = 6.886$, $p = 0.003$, $\eta^2_p = 0.271$). Tukey's post-hoc tests showed that the deviation of subjects in experiment 3 was much smaller than the Hit ($t = -3.579$, $p = 0.003$, Cohen's $d = -1.432$) and Miss ($t = -2.932$, $p = 0.015$, Cohen's $d = -1.369$) participants of experiment 1. This indicated that these subjects reverted towards baseline performance more rapidly. This difference was also evident on the early ($F(2,37) = 10.435$, $p < 0.001$, $\eta^2_p = 0.361$; post-hoc tests: Hit vs exp. 3 group: $t = -4.458$, $p < 0.001$, Cohen's $d = -1.529$; Miss vs exp. 3 group: $t = -3.475$, $p = 0.004$, Cohen's $d = -1.785$) and late ($F(2,37) = 8.55$, $p < 0.001$, $\eta^2_p = 0.316$; post-hoc tests: Hit vs exp 3 group: $t = -4.009$, $p < 0.001$, Cohen's $d = -1.48$; Miss vs exp 3 group: $t = -3.215$, $p = 0.007$, Cohen's $d = -1.516$) feedback washout trials. In fact, average hand deviation of the subjects of experiment 3 was close to zero on the feedback washout trials,

while that of the Hit and Miss participants continued to be much larger. As we have argued in the main manuscript, the subjects in our third experiment compensated for the imposed performance error by employing a deliberative re-aiming strategy. As such, this strategy (of aiming away from the original target) would be irrelevant on washout trials. The highly transient nature of after-effects suggests that strategy use was rapidly "abandoned" by these subjects when it was no longer relevant.

3. Alternative model in which performance errors directly modulate prediction error driven implicit learning

The results of experiment 1 revealed clear differences between the hand angles of the Hit and Miss groups. As described in the main manuscript, these differences could be accounted for in a mathematical model in which performance errors and sensory prediction errors drive independent implicit processes that sum to produce the net change in behavior. Here we consider another framework that can also account for the behavioral differences between these two groups. In this "interaction" model, adaptation is driven solely by sensory prediction errors, but can be modulated by the presence of performance errors. Specifically, task failure could amplify prediction error driven changes in motor output[3–5], ultimately producing greater total learning. The corresponding model equation is:

$$x(n+1)= C_A * A_{SPE} * x(n) + C_B * B_{SPE} * SPE$$

Here, x represents the internal state, SPE signifies the sensory prediction error, A and B are the retention factors and error sensitivity respectively, and C_A and C_B represent parameters that modulate them. For the Miss group, C_A and C_B can be set as 1, while they can be estimated from model fits for the Hit group (C_A and C_B can also be set as 1 for the Hit group and estimated for the Miss group). Further, since the SPE remains constant in the error clamp, B*SPE can be estimated as a single term. This model also predicts differences between the Hit and Miss groups (Figure S2a).

We first fit the model to the data of the Miss group and estimated the values of A_{SPE} and the B_{SPE}*SPE (C_A and C_B were set to 1). We then used these estimates when fitting the model to the data of the Hit group and estimated the values of C_A and C_B. Both model fits are shown in Figure S2b. We found that while C_A did not change substantially from 1 (estimated C_A = 1.153), C_B was ~7.14 times smaller. This suggested that the absence of a performance error in the Hit group strongly attenuated the sensitivity to the sensory prediction error. This reduced sensitivity resulted in much smaller updates to the state estimate, ultimately producing smaller changes in net motor output.

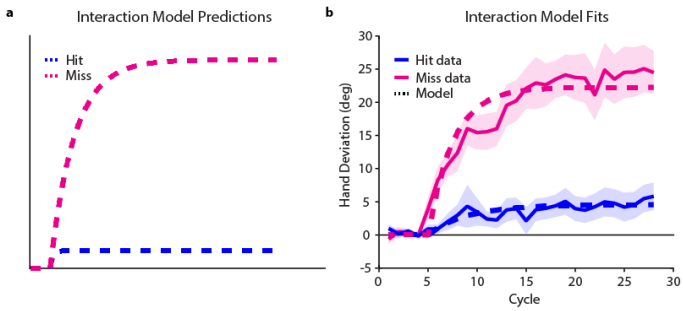

Figure S2: interaction model: predictions and fits. (a) *Simulated hand deviation derived from a model where a sensory prediction error (SPE) induces implicit learning while a task performance error (TPE) modulates it. This model predicts greater learning for the Miss than the Hit group.* ***(b)*** *Model fits to the data of experiment 1. Solid lines represent the experimentally observed hand deviation (shaded region denotes SEM), while the dashed lines represent the model fits. The model was first fit to data from the Miss group with C_A and C_B set to 1. We obtained a good fit with an R^2 = 0.89 and RMSE = 2.819. The estimated parameter values were: A_{SPE} = 0.6735 and B_{SPE}*SPE = 7.2607. Then, the model was fit to data of the Hit group (R^2 = 0.79, RMSE = 0.772) to estimate C_A and C_B. The values obtained were C_A = 1.153 and C_B = 0.1401.*

It is clear that this interaction model can account for the differences between the Hit and Miss groups of experiment 1. The nature of this interaction is such that performance errors directly affect the implicit learning process. This then implies that such errors do not necessarily trigger a different process on their own. However, our second and third experiments strongly suggest that performance errors do in fact set in motion a *different*, intentional mechanism that takes the form of a strategic re-aiming process, rather than acting directly on implicit learning itself. In other words, our findings suggest that two separable mechanisms – one related to cognitively-assisted strategy use and the other to implicit recalibration – combine in an additive manner to produce behavioral changes. Whether there exist certain conditions in which performance errors do in fact act directly on the implicit process, remains an open question.

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