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MOTOR LEARNING DRIVEN BY SENSORY PREDICTION ERRORS IS INSENSITIVE TO TASK PERFORMANCE FEEDBACK

Gaurav Panthi[1], Pratik Mutha[1,2]*

[1]Department of Cognitive and Brain Sciences, Indian Institute of Technology Gandhinagar, Gujarat – 382355, India.

[2]Department of Biological Sciences and Engineering, Indian Institute of Technology Gandhinagar, Gujarat – 382355, India.

***Corresponding author**: pm@iitgn.ac.in

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ABSTRACT

Accurate motor behavior relies on our ability to refine movements based on errors. Sensory prediction errors (SPEs), arising from discrepancies between expected and actual sensory feedback, are a primary driver of motor adaptation. Task performance errors (TPEs), reflecting failures to achieve movement goals, also influence learning. However, whether and how these errors interact to shape net learning, remains controversial. This controversy stems from difficulties in experimentally decorrelating SPEs and TPEs, ambiguity related to interpretations of task instructions, and inconsistencies between theory and computational models. To address this, we employed variants of an “error-clamp” adaptation paradigm across arm reaching experiments in humans of either sex. Addressing the ambiguity of whether the TPEs are ignored in standard clamp designs as assumed in theoretical (but not computational) models, experiment 1 manipulated TPE magnitude by varying the endpoint feedback location while holding SPE constant. We found that learning was uninfluenced by TPE size. Experiment 2 assumed that the TPE is in fact disregarded under clamp instructions. To then study SPE-TPE interactions, we induced TPEs of varying sizes by “jumping” the target while always clamping cursor feedback towards the original target. Instructions to reach in the direction of the new target also then induced an SPE. Crucially, learning driven by this SPE was unaffected by TPE magnitude, a result validated by two additional experiments. Together, these results provide converging evidence that SPE-mediated learning remains impervious to variations in task performance feedback, and point to a distinction in learning mechanisms triggered by these two error signals.

SIGNIFICANCE STATEMENT

Humans improve their motor performance by learning from errors. This work aimed to resolve a long-standing controversy about how two error signals, task performance errors (TPEs) and sensory prediction errors (SPEs), interact during motor learning. Employing novel paradigms to isolate these errors, we demonstrate that SPE-driven learning is unaffected by variations in TPE magnitude. Our results challenge models proposing synergistic or competitive interactions between these two errors and suggest distinct mechanistic contributions of these error signals to motor learning.

INTRODUCTION

The constantly changing environment we interact with introduces errors in our actions. The sensorimotor system recalibrates motor plans to account for such errors, a process termed motor adaptation. Laboratory experiments of adaptation (Kumar et al., 2020; Morehead et al., 2017; Sainburg et al., 1999; Shadmehr and Mussa-Ivaldi, 1994) have focused largely on two sources of error: a sensory prediction error (SPE) and a task performance error (TPE). An SPE is operationalized as a mismatch between actual and predicted sensory feedback of motion, while TPEs correspond to failures in achieving the task goal, such as a feedback cursor failing to strike a reach target. Our goal here is to understand how SPEs and TPEs interact during adaptation, an issue laden with highly inconsistent research outcomes (Al-Fawakhiri et al., 2023; Kim et al., 2019; Leow et al., 2018; Oza et al., 2024; Tsay et al., 2022).

A fundamental problem in using canonical adaptation paradigms for probing SPE-TPE interactions is that these two errors are inherently correlated in them. For example, in visuomotor rotation tasks, wherein visual feedback of the movement (cursor) is rotated relative to actual hand motion, SPE and TPE magnitudes are tightly linked, and a reduction in one leads to a concomitant decrease in the other. This issue can be partially mitigated using "error-clamps", in which the cursor moves in a fixed direction, completely de-yoked from the hand. Participants are instructed to ignore the cursor and move their hand to the target, yet the hand gradually drifts and aftereffects emerge (Morehead et al., 2017). These changes have been interpreted as being SPE-driven because cursor motion is dissociated from task success. However, in such paradigms, the extent to which task-outcome-related information is truly eliminated remains unclear. For example, a cursor persistently deviating away from the target may also signal impending task failure (TPE). Indeed, prior clamp studies have shown that SPE-driven adaptation is larger when a TPE is present than when it is not, and computational models of clamp behavior often include a TPE term, acknowledging its presence (Oza et al., 2024; Tsay et al., 2022). Yet, the view that such learning is SPE-driven, and the discrepancy between this theory and modelling, raises questions about the appropriateness of the standard clamp paradigm for studying SPE-TPE interactions.

To better address this, we consider two possibilities. First, that in typical error-clamps, the TPE is unambiguously present and is *not* ignored. If so, then this paradigm is not ideal for probing TPE influence on SPE-driven learning since these two error signals remain not only correlated but also unchanged as people learn. To overcome this limitation, we modified the error-clamp paradigm such that the clamped cursor disappeared midway through the reach, enabling

participants to perceive the SPE. However, the TPE magnitude was varied by re-displaying the cursor at the reach endpoint but at different distances relative to the target. Thus, by keeping SPE fixed and systematically manipulating the TPE, we probed if and how TPEs influence SPE-mediated learning.

The second possibility is that the TPE in conventional clamps is indeed ignored when participants are so instructed. If so, then standard clamp paradigms are again poorly suited for probing SPE-TPE interactions. We therefore turned to our new paradigm (Oza et al., 2024) wherein we "jump" the target while clamping the cursor towards the original target. Participants re-aim towards the new target, and an SPE emerges "on the fly" because participants expect the cursor to follow the redirected hand but instead observe it moving towards the original target. Importantly, the task-performance-related signal in this paradigm is based on the requirement to modify hand motion relative to an updated task goal rather than on explicit visual confirmation of hand success. To assess how the magnitude of this signal influences the ensuing SPE-driven adaptation, in our second set of experiments, we manipulate the amplitude of the target jumps and instruct participants to respond by aiming towards the new target.

MATERIALS AND METHODS

Participants

A total of 144 young, healthy, right-handed adults (age range: 18-35 years, 38 female) were recruited for different experiments in this study. Handedness was assessed via the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided written informed consent to participate in the study and were monetarily compensated for their time. The experimental protocols were approved by the Institute Ethics Committee of the Indian Institute of Technology Gandhinagar.

Experimental setup

The experiments in this study were conducted using two different setups. For our first experiment, we used the Kinarm end-point robotic manipulandum (Kinarm, Canada) which consisted of a virtual reality system with a high-definition TV screen mounted horizontally above it (Figure 1a). Participants sat in an adjustable chair, facing the Kinarm system, and held the handle of a robotic arm, which allowed planar movements only. A mirror positioned

between the robot and the TV display reflected the task presented on the screen while obstructing the direct vision of the hand. A circular cursor displayed on the screen provided visual feedback regarding the position of the hand (handle of the robotic system). This setup also allowed us to manipulate and differentiate the motion of the displayed cursor from the actual hand movement. Our remaining experiments were conducted using a digitizing tablet system (GTCO Calcomp, Scottsdale, AZ), which also employed a pseudo virtual reality setup similar to the Kinarm but differed in how movements were recorded (Figure 2a). Here, participants made planar movements on the tablet surface using a hand-held stylus, with a cursor on the screen providing visual feedback of their hand position. Again, a mirror placed between the tablet and the screen blocked vision of the arm. This too enabled us to dissociate the displayed location of the hand (cursor) from its actual position.

Given that even relatively small visuomotor latencies can influence motor performance and learning, we estimated the end-to-end visuomotor latency of our custom tablet-based setup using the procedure described by Hadjiosif et al. (2025). The estimated latency was 58 ms, consistent with values reported for similar systems earlier (Brudner et al., 2016; Honda et al., 2012). The visuomotor latency for the Kinarm system has previously been estimated to be approximately 48 ms (McKenna et al., 2017).

Task Design

All our experiments required participants to make reaching movements from a stationary start circle towards a target with their dominant, right arm. To begin a trial, participants first brought the cursor inside the start circle. After a delay of 500 milliseconds, a circular target appeared on the screen, and participants were told to make a quick slicing movement through the target rather than stopping at it. During these movements, participants received one of three types of cursor feedback: veridical, clamped or no feedback at all. On veridical feedback trials, the cursor accurately represented the hand position, whereas the cursor remained invisible during no-feedback trials. On error-clamp trials, the cursor followed an invariant trajectory rotated by a specific angle, regardless of the direction in which the participant moved their hand. Importantly, participants were explicitly informed about the nature of the cursor feedback on such trials and were instructed to ignore it, focusing instead on moving their hand toward the target.

Experiment 1: In experiment 1, participants (n = 36) performed 380 reaches originating from the start circle (2 cm diameter) to one of four targets (2 cm diameter) located at a distance of 12 cm at one of the locations (45°, 135°, 225° and 315°) arranged around an imaginary circle. Target presentation was pseudorandom with a target appearing once in a cycle of 4 trials. The task consisted of 3 continuous blocks of trials: baseline (60 trials), learning (280 trials) and washout (40 trials). The experiment began with a block of familiarization trials to get participants to understand the task better. Following familiarization, participants performed baseline trials, comprised of 3 sub-blocks of 20 trials each: no feedback, partial feedback, and veridical feedback. In the "no feedback" sub-block, the cursor was not shown during the reach. In the "partial feedback" sub-block, the cursor remained visible only up to half the distance to the target (6 cm) and then disappeared. It was re-displayed as an endpoint once the hand crossed the target distance (12 cm) for a duration of 1 second. Finally, in the "veridical feedback" sub-block, the cursor remained aligned with the hand. Following the baseline block, participants underwent 280 trials of learning. Learning trials were identical to the "partial feedback" trials of the baseline sub-block, except that the cursor motion was artificially "clamped" at a fixed angle of 30° relative to the target direction (Figure 1b). Both clockwise (CW) and counterclockwise (CCW) perturbations were used with counterbalancing across participants. Participants were instructed to ignore the cursor and slice their hand through the target. Cursor feedback persisted until the hand reached the midpoint (6 cm) of the distance to the target, at which point it was extinguished. This deliberate perturbation of cursor feedback, irrespective of actual hand motion, induced a consistent sensory prediction error (SPE) throughout the learning block. Once the hand crossed the target distance of 12 cm, the cursor was immediately redisplayed for 1 second at a single endpoint location at one of three predefined distances from the target: 0°, 15°, or 30°. The specific end-point angle depended on the group to which participants were assigned (n = 12 each). The distance from the target to this endpoint cursor location represented the task performance error (TPE). Importantly, this experimental design facilitated the separation of task error from sensory prediction error, where the TPE was induced by displaying end-point feedback at different locations (TPEs) while the SPE was produced through the clamped cursor feedback. Also note that the 15° and 30° TPE groups were never actually successful in making the cursor hit the target, while the 0° group was always successful (despite the SPE of 30°). Following learning, participants performed 40 washout trials, which comprised of 20 "no-feedback" and 20 "veridical feedback" trial sub-blocks, like in the baseline block. On these trials, participants were again instructed to slice their hand through the target.

Control experiment: To further examine whether persistent TPEs could account for the observed adaptation in clamp paradigms, we performed a control experiment in which participants received feedback about the cursor-target discrepancy either immediately upon crossing the specified movement distance ("No-delay"), or 2 seconds after trial completion ("Delayed"). However, unlike experiment 1, in this control experiment, the cursor was displayed as an endpoint (and not continuously during the movement) at a fixed, 20° angular offset relative to the target direction ("endpoint clamp"). This resulted in a persistent cursor-target discrepancy in both groups. Participants were instructed to ignore the feedback and slice their hand through the target. We reasoned that if task failure alone were sufficient to drive adaptation, then the Delayed feedback group should adapt despite disruption of the temporal relationship between movement and its sensory consequences. The methodological details for this experiment are provided in Text S1.

Experiment 2: In experiment 2, 36 participants were recruited to one of the three groups (n =12 each) and performed reaching movements from a circular start position (0.9 cm diameter) to one of the eight targets (0.98 cm diameter) located radially at a distance of 10 cm. This task involved performing reaches across 3 continuous blocks: baseline, learning, and washout. Both, the baseline and the washout blocks comprised of 2 sub-blocks: no feedback and veridical feedback. In the "no-feedback" sub-bock, participants performed reaches without any online cursor information, while in the "veridical feedback" sub-block, the cursor was visible and was aligned to the hand motion. Following baseline, participants performed 240 learning trials on which the target location was shifted ("jumped") by a predetermined angle of either 10°, 15°, or 20° (n = 12 each) once the cursor covered a 2 cm distance from the start position (Figure 2b). This was implemented by extinguishing the original target and displaying a new one at the specific location, thus creating the impression that the target had "jumped". Jumps could be clockwise (CW) or counterclockwise (CCW) (counterbalanced across participants). Importantly, on these trials, the cursor remained clamped in the direction of the original target, but participants were asked to ignore it and instead slice their hand through the new target. Once the hand crossed the specified target distance, the cursor was extinguished but remained frozen at its last displayed location until trial end. The shift-induced TPE required participants to adjust their movement direction across trials, thereby introducing goal-related behavioral demands. Critically, the difference in the expected motion of the cursor as they moved their hand in the direction of the new target and its actual motion in the direction of the old target also induced an SPE. This disparity subsequently drove additional gradual changes in hand angle. Following learning, participants performed 40 washout trials (20 no-feedback and 20 veridical feedback). During the "no-feedback" trials, participants were instructed to

avoid use of any strategies they might have used and move their hand straight through the target.

Experiment 3: In this experiment (n = 36), participants moved from a start position (0.9 cm diameter) to one of the eight targets (0.98 cm diameter) located at a radial distance of 10 cm. After a few familiarization trials, participants performed 40 baseline trials, where the cursor was aligned with their hand. This block was subdivided into two sub-blocks: no feedback (first 20 trials) and veridical feedback (remaining 20 trials). Following baseline, participants performed 240 learning trials. During these trials, the target was "jumped" to a new location that was either 10°, 15°, or 20° (n = 12 each) CW or CCW (counter-balanced) from the original location (Figure 3a). Participants were instructed to make accurate slicing movements through the new target without stopping at it. Importantly, cursor feedback remained veridical throughout the learning block. As in experiment 2, once the hand crossed the target distance, the cursor was extinguished but remained frozen at its last displayed location until the end of the trial. After learning, participants performed a washout block of 40 trials, which were similar to baseline (sub-blocks of 20 no-feedback trials and 20 veridical feedback trials). At the beginning of the washout block, participants were instructed to avoid using any strategy they might have developed during the learning trials and move their hand through the (original) target directly.

Experiment 4: In experiment 4, the general experimental procedures were identical to experiment 2, except for the learning block. Participants (n = 36) were randomly assigned to three groups and performed reaching movements to one of the eight targets that appeared at a 10 cm distance. During learning trials, as participants moved a 2 cm distance, the target was "jumped" to a new location at 10°, 15°, or 20° (CW or CCW, counterbalanced) while the cursor remained clamped in the direction of the original target. While this was a general feature of the entire learning block, the learning trials appeared in sub-blocks that differed in terms of what the participants were expected to do. These sub-blocks were presented in an alternating set of 16 trials each (Figure 4a). In the first "learning" sub-block, participants were asked to ignore the cursor and slice their hand through the new target. As in experiment 2, this was expected to lead to a rapid change in hand angle as participants deliberately aimed away, which would then additionally induce an SPE and drive further changes in hand angle. To probe whether this was indeed occurring from the very outset of the learning block, and to understand the broader time-course of SPE-mediated learning, we included a second "test" sub-block, during which participants were asked to ignore the target jump and aim their

movement through the original target. Moreover, on these "test" trials the cursor feedback was completely eliminated. This enabled us to understand *when* the changes in hand angle mediated by the SPE induced online on the "learning" sub-block trials were coming into effect. Following the learning block, participants performed 40 washout trials similar to those in experiment 2. During these trials, they were instructed to move their hand directly through the target avoiding any aiming strategy that they might have used during learning.

Data analysis

Recorded X-Y hand position data were first filtered using a Butterworth filter with a cutoff frequency of 10 Hz. Velocity values were subsequently obtained by differentiating the filtered position data. The primary dependent variable in this study was the change in hand angle across trials. Hand angle was defined as the angle between two vectors: one connecting the start position to the target, and the other connecting the start position to the hand position at peak velocity. Outliers during the baseline block were identified as trials in which participants either failed to initiate a movement or produced hand angles exceeding ±20°. To correct for individual directional biases, the mean baseline hand angle for each participant was subtracted from all trials of that participant. Next, outliers during learning and washout blocks were identified. These included trials in which participants failed to initiate a movement, as well as trials flagged using a moving median filter procedure. Specifically, for each trial, the local median and median absolute deviation (MAD) were computed using a window of 8 surrounding trials on either side of the current trial (excluding the current trial itself). The MAD was converted to a robust estimate of standard deviation (σ_{robust} = 1.4826 x MAD), and trials were classified as outliers if their values exceeded ±4.5 x σ_{robust} relative to the local median. Across all trials (including baseline trials) from the main experiments (excluding the control experiment), a total of 1.797% of trials were excluded.

Adaptation was quantified as the change in these baseline-corrected and outlier-excluded hand angles across the learning block. Early learning was defined as the mean hand deviation over the first 32 learning trials, i.e., 8 cycles in experiment 1 and 4 cycles in experiment 2, 3 and 4. Similarly, final learning was also defined as mean hand deviation over the last 32 learning trials. Aftereffects magnitude was quantified as average hand deviation of the first 16 trials of the no-feedback washout sub-block. In experiment 1, we also calculated learning rate by first bootstrapping the learning data and then fitting an exponential of the form [$y = ae^{-bx} + c$] to each bootstrapped sample. For the statistical comparisons one-way ANOVA, one sample t-tests and linear mixed-effects model were used. For the linear mixed-effects model employed

in experiment 4, the no feedback baseline and the first three no-feedback test sub-blocks and group were used as fixed-effects, and participants were used as random-effects, allowing them to have random intercepts and slopes. The significance threshold was set at 0.05.

RESULTS

Experiment 1

In our first experiment, 3 groups of participants participated in a modified error-clamp paradigm in which we extinguished the clamped feedback cursor at the halfway point to the target (Figure 1b). After the full target distance had been covered, we re-displayed the cursor at either 0° (TPE0° group), 15° (TPE15° group) or 30° (TPE30° group) from the target. Thus, while the SPE remained fixed, the TPE could be varied. We compared the change in hand angle (hand deviation) and learning rate across the three groups to probe whether the TPEs of different magnitudes would influence the amount of learning driven by the SPE. Broadly, we found no group differences in adaptation.

Figure 1c shows that three groups displayed typical adaptation curves and reached asymptote with repeated practice. There was no group difference ($F_{2,33}$ = 0.172, p = 0.843, η^2_p = 0.010; BF_{10} = 0.213) in hand deviation during the early learning phase (Figure 1d, mean ± sem: TPE0° = 6.779 ± 0.549°, TPE15° = 6.850 ± 1.173°, TPE30° = 6.165 ± 0.896°). Across participants, median (±IQR) reaction times were slightly greater than 300 ms during early learning (TPE0° = 317 ± 51.37, TPE15° = 334 ± 103, TPE30° = 339.75 ± 41.5), but this was not too different from values observed during baseline (TPE0° = 310.25 ± 25.62, TPE15° = 302.25 ± 58.37, TPE30° = 314.5 ± 62.37). Hand deviation during late learning (Figure 1e) was also comparable across the three groups (mean ± sem: TPE0° = 20.397 ± 1.407°, TPE15° = 20.166 ± 1.743°, TPE30° = 18.721 ± 1.729°; $F_{2,33}$ = 0.309, p = 0.736, η^2_p = 0.018; BF_{10} = 0.233). This preliminarily indicated that the magnitude of the TPE did not influence learning in our task. To probe this better, we also compared aftereffects across the groups. Mean aftereffect magnitude was 16.388 ± 1.178°, 15.975 ± 1.501° and 17.358 ± 1.685° for the TPE0°, TPE15° and TPE30° groups respectively. Again, group differences were non-significant (Figure 1f, $F_{2,33}$ = 0.233, p = 0.793, η^2_p = 0.014; BF_{10} = 0.222), indicating that adaptation remained invariant despite variations in the TPE.

Could TPEs have influenced the rate of learning than just the initial and final hand angle or aftereffects? To address this, we compared the learning rate across the three groups (Figure 1g). We fit a single rate exponential function of the form [$y = ae^{-bx} + c$] to 10000 bootstrapped samples of hand deviation for each group and obtained the learning rate. However, there were no group differences as indicated by the overlap in the 95% confidence intervals of the bootstrapped distributions (TPE0° = 0.0696-0.1254, TPE15° = 0.0490-0.1066, TPE30° = 0.0663-0.1072). Collectively, these findings of this experiment suggested that TPEs of different magnitudes did not differentially influence adaptation to the SPEs induced by the error-clamp.

To probe whether persistent task failure alone could account for the learning seen in clamp paradigms, we performed an additional control experiment using delayed endpoint-clamped feedback. These results, presented in Text S1, showed that adaptation was abolished when the endpoint clamp was delayed (Figure S1) despite the continued presence of a clear cursor-target discrepancy.

Experiments 2 and 3

In our second experiment, TPEs were induced by jumping the reach target by 10° (TPE10°), 15° (TPE15°) or 20° (TPE20°) but the cursor was clamped in the direction of the original target (Oza et al., 2024). This design produced a TPE as the cursor always missed the jumped target location (Figure 2b). Participants were asked to respond by aiming their hand towards the new target, but since the cursor was clamped towards the original target, an SPE was also induced. Note that this SPE came about due to the mismatch between the expected and actual direction of cursor motion; that is, participants expected the cursor to go with the hand towards the new target, but it actually traveled in the direction of the original target. Our main question of interest was whether learning driven by SPEs would differ across our three groups.

Figure 2c shows the hand trajectories of representative participants from each group, during the early and late learning phases. All participants demonstrated rapid changes in movement direction in the direction of the new target from the outset itself. These adjustments also appeared to scale with jump magnitude and were consistent with participants adopting goal-directed re-aiming responses to accommodate the changed target location. Consistent with this, across participants, median reaction times increased to 591.67 ± 216.67 ms, 643.75 ± 125 ms and 612.5 ± 133.33 ms during early learning from 441.67 ± 79.17 ms, 483.33 ± 134.37

ms and 439.58 ± 101.04 during baseline for the TPE10°, TPE15° and TPE20° groups respectively. Figure 2d shows the overall learning curve for the three groups. It is evident that within a few trials, hand deviation exceeded the angle by which the target had been jumped; this trend to "overcompensate" beyond the jump magnitude was evident across all 3 groups (mean ± sem: TPE10° = 11.935 ± 1.702°, TPE15° = 20.552 ± 2.387°, TPE20° = 24.307 ± 2.459°), and group differences at the early learning phase (Figure 2e) were statistically significant ($F_{2,33}$ = 8.244, p = 0.001, η^2_p = 0.333).

As participants continued to aim for the new target, the induced SPE caused further changes in hand angle, albeit more gradually in all groups. By the end of learning, all participants demonstrated significant hand deviation with notable differences evident between groups (Figure 2f, mean ± sem: TPE10° = 21.596 ± 1.238°, TPE15° = 28.775 ± 2.392°, TPE20° = 40.487 ± 2.538°; $F_{2,33}$ = 19.922, p < 0.001, η^2_p = 0.547). We also observed a non-zero aftereffect during the early washout trials (Figure 2g), likely arising from implicit learning triggered by this SPE (Oza et al., 2024). Notably, there were no group differences in its magnitude (mean ± sem: TPE10° = 6.047 ± 0.896°, TPE15° = 6.126 ± 1.050°, TPE20° = 8.260 ± 1.242°; $F_{2,33}$ = 1.371, p = 0.268, η^2_p = 0.077; BF_{10} = 0.470), suggesting again that there was no impact of TPE size on SPE-based learning. Although the magnitude of these aftereffects was smaller than that observed in experiment 1, the critical observation was that they remained comparable across target-jump magnitudes.

However, we wondered whether there might be subtle differences in the SPE-mediated learning that might be sensitive to TPE magnitude that occurred during the course of adaptation which the aftereffect could not capture. If so, then group differences would be evident when the SPE-mediated component is isolated from the combined effect of aiming towards the new target and the adaptation to the SPE induced thereby. To begin isolating the SPE-mediated component, in our third experiment, we first measured the change in hand angle that would result from re-aiming to a new target location. To do so, we measured the change in hand angle in response to target jumps alone under conditions of veridical (instead of clamped) cursor feedback (Figure 3a).

Three groups of participants performed point-to-point reaching movements with the cursor aligned accurately with actual hand motion. During learning trials, the target was shifted by 10° (TPE10°), 15° (TPE15°), or 20° (TPE20°) to induce TPEs, and participants were instructed

to make their movement through the new target. Across all groups, participants rapidly adjusted their hand trajectories toward the shifted target (Figure 3b), and reached asymptote rapidly (Figure 3c). Correspondingly, median reaction times increased to 429.17 ± 216.667 ms, 483.33 ± 171.87 ms and 493.75 ± 280.21 ms from baseline values of 393.75 ± 179.17 ms, 435.42 ± 76.04 ms and 427.08 ± 104.17 ms for the TPE10°, TPE15° and TPE20° groups respectively. As in experiment 2, hand deviation was evidently different across the groups during the early learning phase itself (Figure 3d, mean ± sem: TPE10° = 5.036 ± 1.194°, TPE15° = 10.054 ± 1.430°, TPE20° = 12.773 ± 2.000°; $F_{2,33}$ = 6.187, p = 0.005, η^2_p = 0.273). Participants showed near complete compensation of the target jump within a few trials, and only incremental changes in hand angle thereafter. At the end of learning (Figure 3e), the hand deviation reached 7.822 ± 0.701°, 12.761 ± 0.524°, 18.365 ± 0.924° on average for the 10°, 15° and 20° groups respectively. The difference in hand angle across the three groups at the end of learning was statistically reliable ($F_{2,33}$ = 51.508, p < 0.001, η^2_p = 0.757). This indicated that participants effectively adapted their movements to account for the jump-induced TPE (Sadaphal et al., 2022). Importantly, unlike experiment 2, no overcompensation was observed in response to target jumps. During washout, when participants were instructed to move directly towards the original target, small aftereffects were observed (mean ± sem: TPE10° = 1.809 ± 0.535°, TPE15° = 1.774 ± 0.667°, TPE20° = 2.209 ± 0.791°). Comparisons of aftereffect magnitude relative to no-feedback baseline trials using Wilcoxon signed-rank tests revealed a small but significant aftereffect in the TPE10° group (W = 12, p = 0.034, r = 0.692, BF_{10} = 1.071), while the TPE15° and TPE20° groups showed only marginal effects (TPE15°: W = 15, p = 0.064, r = 0.615, BF_{10} = 2.083; TPE20°: W = 16, p = 0.077, r = 0.590, BF_{10} = 1.744). Importantly however, the target was sufficiently large (angular radius of 2.81 degrees) that these small directional biases still placed the hand well within the target boundaries in all groups (Figure 3c).

Since our larger aim was to isolate the SPE-mediated learning in experiment 2, we proceeded to subtract out, for each jump magnitude separately, the average TPE-mediated learning of the early learning phase of experiment 3 from the learning observed in experiment 2. We reasoned that this might partially account for the rapid target-jump-related compensation component present in experiment 2, i.e., the component that was due to the explicit re-aiming towards the new target. Upon doing so, we obtained “learning curves” in which group - differences were still evident (Figure 3f), and also statistically significant at the end of the learning phase ($F_{2,33}$ = 7.667, p = 0.002, η^2_p = 0.317; Figure 3g). Note though that because these comparisons involved different participant groups and task conditions, this subtractive

analysis should be interpreted cautiously and only as a heuristic estimate rather than a formal decomposition of learning processes.

One possible interpretation of these residual group differences is that they reflect differences in SPE-mediated learning as a function of TPE magnitude. In other words, these group differences might provide evidence for the modulation of implicit learning by task errors. However, we also noted that the removal of the jump-mediated component did not zero out the overcompensation observed in the early learning phase of experiment 2. On average, there was an "additional" hand deviation of 6.899°, 10.498° and 11.534° for the 10°, 15° and 20° target jumps respectively that was still present during the early stages of experiment 2. Moreover, it was unclear whether this overcompensation resulted from continued engagement of deliberative processes in response to the jump-induced TPE (participants trying to "pull" the clamped cursor towards the new target location) or from the SPE induced by the mismatch between hand and cursor motion. Recall that our goal was to remove the TPE-mediated component completely, isolate the SPE-mediated component, and investigate whether this SPE-driven learning was influenced by the TPE. Clearly, this subtractive approach was limited in doing so. It therefore became imperative to develop a more direct method for probing implicit learning without relying on subtractive assumptions, even if participants were overcompensating initially. We proceeded to do so in experiment 4.

Experiment 4

The experimental design for our fourth and final experiment was similar to that of experiment 2 but included intermittent sub-blocks of 16 test trials each alternating with learning sub-blocks of 16 trials each (Figure 4a). On the test trials, the cursor feedback was eliminated, and participants were instructed to ignore the target jump and reach towards the original target. Inserting these trials was important since it enabled us to probe the evolution of SPE-mediated changes in hand angle – we expected that as adaptation progressed, participants would show a bias towards the trained direction (rather than moving in the direction of the original target) on these test trials. At the same time, the learning sub-blocks allowed us to obtain overcompensation identical to experiment 2 in the early learning phase, but how this overcompensation came about would be irrelevant. Rather, our key comparison would be the magnitude of the bias across the different groups.

Figure 4b shows the change in hand angle for the three groups during the learning and test sub-blocks. For comparison, the same data is overlaid with the hand deviation data of the three groups of experiment 2 in Figure 4c. As is evident, there was rapid and robust overcompensation in all groups, with the average change in hand angle being 13.805 ± 1.187°, 16.428 ± 2.3°, 23.377 ± 2.455° ($F_{2,33}$ = 5.767, p = 0.007, η^2_p = 0.259) during the early learning phase for the 10° (TPE10°), 15° (TPE15°), and 20° (TPE20°) jump groups respectively (Figure 4d). As learning progressed, there was an increasing trend in the hand deviation. At the end of learning, hand angle had increased to 22.395 ± 2.772°, 26.031 ± 2.017° and 36.706 ± 1.939° ($F_{2,33}$ = 10.702, p < 0.001, η^2_p = 0.393) for the TPE10°, TPE15°, and TPE20° groups respectively (Figure 4e). These results were all consistent with the general trend seen in experiment 2.

We then turned our attention to the test sub-blocks (Figure 4f). Firstly, we obtained a small but non-zero "aftereffect" on the first test sub-block 1.956 ± 0.488°, 1.311 ± 0.525°, 2.037 ± 0.883° for the TPE10°, TPE15°, and TPE20° groups respectively. This aftereffect was significantly different from zero in all cases (TPE10°: t(11) = 4.006, p = 0.002, Cohen's d = 1.156; TPE15°: t(11) = 2.497, p = 0.03, Cohen's d = 0.721; TPE20°: t(11) = 2.309, p = 0.041, Cohen's d = 0.666), suggesting that changes in hand angle driven by the SPE had begun to occur during the early learning phase itself. To reiterate, this SPE was induced by the participants' expectation that the cursor would go with the hand as they aimed towards the new target while its actual motion remained clamped in the direction of the original target on the learning trials. Importantly, there were no group differences in hand deviation on the first test sub-block ($F_{2,33}$ = 0.367, p = 0.695, η^2_p = 0.022; BF_{10} = 0.243). This suggested that the SPE-mediated effects were not affected by the TPE magnitude during early learning.

Figure 4f further shows the magnitude of the hand deviation for each group for each of the test sub-blocks, along with the no-feedback baseline as well as the aftereffects, reflecting the time course of implicit learning development from baseline. As can be seen, there was an increasing trend in hand deviation from baseline through the first 3 test sub-blocks for all groups, which was confirmed using a linear mixed-effects model (fixed effect slope = 1.188 [0.658, 1.718], p < 0.001, marginal R^2 = 0.263). However, there was no significant effect of group or interaction between block and group (p > 0.05). The magnitude of hand deviation stabilized after this initial phase for all groups. This mirrored the canonical, SPE-driven change in hand angle that tends to gradually increase over the initial set of learning trials and asymptotes thereafter.

We next asked whether there were any group differences in hand deviation at each sub-block. We did not find this to be the case. Table 1 shows the 95% confidence intervals for hand deviation for each group for each of the 7 test sub-blocks (in addition to the no-feedback baseline sub-block and aftereffects), derived from 10000 bootstrapped samples of the data. The overlap in confidence intervals of the groups at each time point suggests that the degree of implicit adaptation was not different between them even though they experienced different TPEs. In other words, the amount of implicit learning was unaffected by TPE magnitude. Finally, we compared the post-learning aftereffect (Figure 4g) and again found no group differences ($F_{2,33}$ = 0.008, p = 0.992, η^2_p = 4.855 x 10^{-4}; BF_{10} = 0.191), pointing to the fact that implicit learning did not vary with the size of the TPE.

DISCUSSION

For the sensorimotor system to operate effectively, it must learn from errors. During movement, such errors arise from discrepancies between predicted and actual sensory feedback (SPE), or from a failure to achieve the desired task goal (TPE). In this work, we focused on the interaction between these error sources during learning. We employed two new error-clamp tasks that addressed different limitations of the traditional error-clamp paradigm. Our experimental findings suggest that the gradual recalibration typically associated with the SPE remains remarkably robust despite substantial manipulations of task-outcome-related information.

An open issue in motor adaptation research is whether the typical error-clamp paradigm truly isolates the SPE-mediated changes in motor plans, or inadvertently allows task performance (TPE) to influence behaviour. This issue arises because explicit instructions to ignore the cursor do not necessarily guarantee that task-outcome-related information is actually behaviorally (or neurally) ignored. Early variability in hand movement direction, such as abrupt shifts in movement direction opposite to the clamped cursor, suggests that participants might not be able to fully suppress TPE processing. Such adjustments align with the known capacity of a TPE to drive strategic corrections (McDougle et al., 2015; McDougle and Taylor, 2019; Morehead et al., 2015; Sadaphal et al., 2022). Critically, the persistence of such behavior in trials preceding significant SPE-driven adaptation challenges the assumption that clamped paradigms fully dissociate these error signals. Our study overcomes this limitation through two novel approaches: in experiment 1 we assumed that the TPE remains salient in standard

clamps and manipulated the TPE magnitude independent of SPE. In experiments 2 and 4 we bypassed the inherent TPE of error-clamps by inducing TPEs via target jumps, while also creating an SPE on the fly. Our goal was therefore not to create perfectly "pure" SPEs or TPEs, but rather to determine whether systematic manipulations of task-outcome-related information alter the gradual recalibration classically associated with SPE-driven adaptation. The robustness of SPE-mediated learning across both paradigms despite divergent TPE manipulations, supports its primacy in implicit adaptation without any interaction with the TPE. This interpretation is further supported by our control experiment showing that implicit adaptation depends on temporally appropriate sensory prediction discrepancies rather than persistent task failure alone. This of course does not mean that the TPE carries no influence. As a number of recent results, including some of our own have shown, the TPE might set in motion a completely distinct mechanism - volitional, explicitly-accessible adjustments to reach direction (McDougle et al., 2015; McDougle and Taylor, 2019; Morehead et al., 2015; Sadaphal et al., 2022).

Our findings appear to contradict some recent results showing that trial-by-trial learning rates, measured as hand deviation changes between consecutive trials, are modulated by TPE magnitude (Al-Fawakhiri et al., 2023; Tsay et al., 2022). This apparent contradiction brings forth a critical nuance, that the structure of error exposure (blocked vs. random) may determine whether the TPE influences SPE-mediated learning. In our block design, with SPE and TPE relationships fixed across trials, the motor system may treat errors as stable contexts. Under such conditions, SPE-driven adaptation aligns with the implicit mechanism described in classical studies (Mazzoni and Krakauer, 2006; Morehead et al., 2017; Shadmehr and Mussa-Ivaldi, 1994), prioritizing improved sensory prediction over task success. In contrast, in trial-by-trial designs where error magnitudes and their relationships change continuously, TPEs may be interpreted as a dynamic contextual signal that could influence SPE-driven learning. The COIN model (Heald et al., 2021) might be useful in formalizing this idea: when context transition probabilities are high (e.g., random perturbations), the motor system weights TPE more heavily to rapidly adjust strategies, modulating single-trial learning. This implies that in stable environments, SPE-driven recalibration dominates, rendering learning indifferent to TPE magnitude. In contrast, in rapidly changing contexts, the TPE might gate explicit adjustments without altering SPE-based adaptation. Our results thus refine, rather than contradict, prior work, highlighting that the role of the TPE is likely to be context-dependent and largely orthogonal to SPE-driven learning.

Our paradigms also address some inconsistencies between theoretical framing and computational models of the role of TPEs in error clamp paradigms. Specifically, theoretical models suggest that error-clamp paradigms isolate SPE by eliminating or minimizing effects of the TPE (Morehead et al., 2017). However, corresponding computational models include a TPE term (Kim et al., 2019; Tsay et al., 2022). For example, in experiment 4 of Tsay et al. (2022), the target was jumped to different locations while the cursor remained clamped in a fixed direction away from the target. When modeling the ensuing behavior, the TPE was included as the distance between the clamped cursor and the shifted target. Moreover, this TPE included contributions from both the clamp and the target jumps (at least in their "jump away" conditions), which adds an additional layer of complexity to the interpretation as the TPE induced by the rotation (i.e., the clamp) and the TPE induced by a goal shift (i.e., target jump) could engage distinct cognitive or neural mechanisms (Diedrichsen et al., 2005; Mutha et al., 2011a, 2011b). Combining TPEs from multiple origins into a single term within a model, risks obscuring the specific contributions of each type. In our study, this issue was minimized by the use of two distinct task designs: one involving clamp-linked TPEs and another involving jump-induced TPEs. We found no evidence that either type of TPE modulates SPE-driven implicit learning.

Experiments 2 and 4 revealed systematic overcompensation in TPE-mediated re-aiming behavior. Participants adjusted their reaches beyond what was necessary to compensate for the jump, an effect absent when veridical cursor feedback was available in experiment 3 and in our previous work (Sadaphal et al., 2022). One possibility is that, in the absence of visual confirmation of success (due to the cursor being clamped towards the original target), participants continued refining their aiming direction, pausing only when proprioceptive feedback may have signaled excessive hand deviation relative to the jump magnitude. Implicit recalibration was likely simultaneously triggered, driven by the SPE. Importantly, despite differences in TPE-mediated compensation, aftereffects remained indistinguishable across TPE magnitudes in experiments 2 and 4. This again provided confirmation that SPE-driven recalibration remains fundamentally independent of strategic adjustments driven by target jump mediated TPEs.

An additional feature of the present results was that aftereffect magnitudes differed across experiments, being largest in experiment 1 and comparatively smaller in experiments 2 and 4. Importantly, our primary comparisons concerned within-experiment manipulations of TPE magnitude, all of which consistently failed to alter the magnitude of implicit adaptation.

However, the cross-experiment differences may still be informative. It is plausible that the effective SPEs differed across paradigms. In experiment 1, the sensory discrepancy was externally imposed and persistently available during movement execution, whereas in experiments 2 and 4 the SPE emerged indirectly as a consequence of participants progressively re-aiming toward the jumped target while the cursor remained clamped toward the original target. Differences in the stability, salience, or temporal evolution of these discrepancies may therefore have influenced the magnitude of the resulting aftereffects. However, these cross-experiment differences may also relate to competition-based accounts of adaptation (Albert et al., 2022). In experiment 2, participants responded to the target jumps through deliberate re-aiming towards the new target location. As such, a substantial portion of the behavioral correction may have been mediated by this strategic process, potentially leaving less residual discrepancy available to drive gradual SPE-mediated recalibration across trials. In contrast, participants in experiment 1 could not behaviorally "solve" the clamp by re-aiming. Consequently, the prediction-related discrepancy may have remained persistently available throughout learning, potentially contributing to the larger aftereffects observed in that paradigm. Importantly, unlike conventional competition frameworks however, the SPE in our target-jump paradigm of experiment 2 emerged as a consequence of the strategic response itself, likely leading to a more interdependent relationship than in standard rotation tasks. Finally, the intermittent no-feedback test sub-blocks in experiment 4 likely interrupted the accumulation of implicit learning, contributing to the smaller aftereffects observed relative to experiments 1 and 2.

More broadly, our findings support the idea that TPEs and SPEs engage dissociable processes during motor learning. TPEs likely draw upon reward-sensitive cortico-striatal pathways (Diedrichsen et al., 2005; Inoue et al., 2016) associated with explicit strategy adjustments akin to model-free processes involving trial-and-error refinement of actions to achieve immediate success (e.g., re-aiming or mental rotation). Such adjustments prioritize direct behavioral outcomes over internal representations of the environment. In contrast, SPEs involve cerebellar (Galea et al., 2011; Martin et al., 1996; Morehead et al., 2017) and posterior parietal (Kumar et al., 2020; Mutha et al., 2011b, 2017) mechanisms that update internal models of limb-environment interactions, aligning with model-based processes. Here, adjustments are guided by predictive accuracy rather than task success, enabling long-term improvements in sensorimotor control. These processes likely operate in parallel: TPE-driven strategies adjust actions to minimize task failure, while SPE-driven adaptation ensures movements remain calibrated to the body's biomechanics and environmental constraints.

641 Collectively, these mechanisms enable robust motor learning across diverse contexts, from
642 immediate goal achievement to sustained environmental interaction.

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FIGURE LEGEND

Figure 1: Experiment 1. (a) Participants performed reaching movements while holding the handle of a robotic manipulandum (Kinarm End-point). The start position, reach targets, and cursor feedback were displayed on a screen and reflected onto a mirror placed horizontally between the screen and the hand, occluding direct vision of the arm. **(b)** Task: Participants reached from the start position towards the target. Feedback was provided by means of a cursor (yellow circle), but motion of the cursor was clamped at a 30° offset from the target direction. Additionally, the cursor was extinguished once the hand crossed a 6 cm distance and was re-displayed when the hand crossed the target distance of 12 cm. The endpoint cursor location could be on the target, or offset by 15° or 30° from the target, thereby creating task performance errors of different sizes. **(c)** Group-averaged hand deviations across cycles for the three experimental groups. Shaded regions represent SEM. **(d–f)** Mean ± SEM hand deviation during (d) early learning, (e) final learning, and (f) no-feedback washout phases. Dots represent individual participants. **(g)** Distributions and box-plots of learning rates for the three groups derived from exponential fits to 10000 bootstrapped hand deviation data samples.

Figure 2: Experiment 2. (a) Setup for experiments 2-4. Participants performed reaching movements on a digitizing tablet using a handheld stylus. The start position, reach targets and cursor feedback were displayed on a screen and reflected on a horizontal mirror placed above the tablet. **(b)** Task: Upon receiving the go cue, participants began a reach, but the originally displayed target was "jumped" from its original location to a new location either 10°, 15°, or 20° away, creating task performance errors (TPEs). At the same time, the cursor was kept clamped in the direction of the original target. Since participants were instructed to reach through the new target, the mismatch between the expected motion of the cursor (aligned with the hand) and the actual motion of the cursor (clamped towards the original target) induced an SPE. **(c)** Example hand trajectories for one of the eight targets from a representative participant. Only the first 10 cm of the trajectory is shown. Early learning trials are plotted using dotted lines, whereas late learning trials are plotted using solid lines. **(d)** Group-averaged hand deviation across cycles for the three groups. Shaded regions represent SEM. **(e–g)** Mean ± SEM hand deviation during (e) early learning, (f) final learning, and (g) no-feedback washout phases. Dots represent individual participants.

Figure 3: Experiment 3. (a) Task: As in experiment 2, the initially displayed reach target jumped by 10°, 15°, or 20°, inducing TPEs. Participants were instructed to slice through the new target without stopping at it. The cursor remained aligned with the hand all the time. **(b)** Example hand trajectories for one of the eight targets from a representative participant. Only the first 10 cm of the trajectory is shown. Early learning trials are plotted using dotted lines, whereas late learning trials are plotted using solid lines. **(c)** Group-averaged hand deviations across cycles for the three groups. Shaded regions represent SEM. **(d–e)** Mean ± SEM hand deviation during (d) early learning and (e) final learning. Dots represent individual participants. **(f)** Hand deviation computed by subtracting the initial adaptation levels of experiment 3 from all cycles of experiment 2. **(g)** Mean hand deviation at the end of the learning period for the "learning curves" in (f).

Figure 4: Experiment 4. (a) Task: Participants performed baseline (no perturbation movements) followed by a learning block composed of alternating sub-blocks of learning and test trials. The learning sub-blocks were identical to those experiment 2, wherein participants reached in the direction of a "jumped" target while cursor feedback remained clamped in the direction of the original target. During the test sub-blocks, cursor feedback was withheld, and participants were instructed to ignore the target jump and aim towards the original target location. Learning and test sub-blocks thus differed in terms of whether participants aimed in the direction of the new target or the original one. **(b)** Group-averaged hand deviations (calculated relative to the original target direction) across cycles for the three groups. **(c)** Hand deviation data from experiment 2 (dotted lines) overlaid for comparison with the data shown in (b). Shaded regions represent SEM. **(d–e)** Mean ± SEM hand deviation during (d) early learning, and (e) final learning. **(f)** Distributions of bootstrapped means and 95% confidence intervals of the hand deviation for each group across the no-feedback baseline, the seven no-feedback test sub-blocks and the aftereffects. **(g)** Mean ± SEM aftereffects. Dots represent individual participants.

778 **TABLE LEGEND**

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780 **Table 1:** 95% confidence interval values of 10000 bootstrapped samples for the three groups
781 for no-feedback baseline sub-block, each test sub-blocks, and aftereffects.

782

783 **TABLE 1**

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Group	no f/b baseline	sub-block 1	sub-block 2	sub-block 3	sub-block 4	sub-block 5	sub-block 6	sub-block 7	efter-effects
TPE10°	-0.63, 0.50	1.09, 2.91	1.81, 4.17	2.57, 4.49	1.92, 5.43	1.86, 4.27	0.73, 3.39	0.75, 2.76	1.40, 4.54
TPE15°	-0.45, 0.94	0.30, 2.26	0.92, 3.35	1.73, 5.30	0.46, 4.03	1.22, 4.42	1.25, 4.00	2.44, 5.62	1.66, 4.45
TPE20°	-0.81, 0.38	0.39, 3.67	0.82, 4.76	2.79, 5.73	2.29, 4.97	2.26, 5.65	2.82, 5.58	1.77, 4.55	1.63, 4.37

Table 1: 95% confidence interval values of 10000 bootstrapped samples for the three groups for no-feedback baseline sub-block, each test sub-blocks, and aftereffects.