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Sensory prediction error drives subconscious motor learning outside of the laboratory

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Abstract

Sensorimotor adaptation is supported by at least two parallel learning systems: an explicit strategy which is intentionally controlled, and an involuntary implicit learning system. These two systems are generally studied in laboratory settings using visuomotor rotations, studies that have shown subconscious learning systems to be driven in part by sensory prediction error (i.e., the mismatch between the realized and expected outcome of an action). Here we used a ball rolling task to explore whether sensory prediction errors can drive implicit motor adaptation outside of the standard and highly constrained laboratory environment. After application of a visual shift, participants rapidly adapted their rolling angles to reduce the error between the ball and target. We removed all visual feedback and told participants to aim their throw directly toward the primary target, revealing an unintentional 5.06° implicit adjustment to reach angles that decayed over time. To determine whether this implicit adaptation was driven by sensory prediction error, we tested participants in a second paradigm similar to Mazzoni and Krakauer (2006) in which participants were given an aiming target that would 'solve' the visual shift. As expected, the aiming group developed a larger explicit strategy increasing their total adaptation. Remarkably, after rapidly reducing ball rolling error to zero, rolling angles in the aiming group gradually drifted over time, resulting in an overcompensation of 3.15° beyond the target (and towards the aiming target). This involuntary drift in rolling angle, which resulted in worsening task performance, is a hallmark of implicit learning driven by sensory prediction error. These results show for the first time that implicit processes driven by sensory prediction error studied in the laboratory actively contribute to motor adaptation in naturalistic skill-based tasks with more complex body motion and interactions with external physical objects.

Introduction

Current theories posit that implicit, i.e., subconscious, motor learning is driven in part by sensory prediction error (SPE): a mismatch between a movement's outcome versus the expected result[1–7]. The notion that errors are a critical implicit learning substrate is central to both descriptive and computational motor control models[1,3,8–10]. The visuomotor rotation (VMR) paradigm has been applied extensively to examine error-based adaptation, in which participants use a robotic manipulandum or tablet to move a cursor towards a virtual target (Fig 1, Inset). A visual rotation is applied to the cursor's path, inducing an SPE. While this constrained environment allows precise error manipulation[2,7], skill learning in natural environments is considerably more complex, involving multiple unconstrained control variables and the use of internal models to predict the

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motion of external physical objects. Do the SPE learning mechanisms uncovered in laboratory settings extend to these more complicated skill-based behaviors? In the rare cases[2,7,11,12] where sensorimotor adaptation has been examined in skill-based settings[13–15], reliable assays to separate implicit learning from explicit (i.e., intentional) strategies have not been applied; these studies have either relied on the tenuous assumption that implicit learning alone persists once a perturbation has been removed, or have attempted to reduce explicit learning by providing aiming instructions, an intervention that could cause the opposite effect: priming explicit adjustments[15]. Furthermore, no attempts have been made to dissociate between error sources that could drive the implicit system, in particular, SPEs versus target (i.e., performance) errors[1,3,7,10,16] which co-occur unless specialized conditions are used to isolate the SPE component.

Here we aimed to fill this gap using a task designed to detect SPE learning within motor actions of ecological relevance. By eliminating target errors and isolating SPEs, we observed an obligatory drift in motor actions, suggesting that subconscious adjustments to everyday movements are driven at least in part by SPEs.

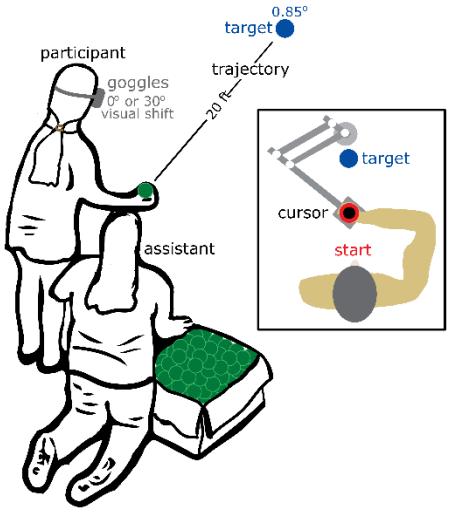

Figure 1. *Unconstrained motor task setup.* Participants wearing goggles with or without a visual shift rolled a tennis ball to a small target 20 feet away on sequential trials. **Inset**. Traditional VMR experiment (adapted from[41])

Results

We trained participants to roll a tennis ball (D = 0.425° at target displacement) towards a small target (D=0.85°) 6.1m away; the ball arrived at the target about 750ms after release (Fig. 1). This paradigm introduced several unconstrained control variables: variations in wrist, elbow, and shoulder angle, bend at the knees and hip, release timing, grip, and arm speed. Further, to internalize sensory error, the brain needed to map visual error between the ball and target onto the participant's temporally separated motion (conditions known to attenuate implicit learning[8,17,18]).

Despite these complex elements, participants achieved excellent performance, hitting the target with high precision (Fig. 2AB, first 40 trials; 0.095° average error [mean across all 27 participants of median error on last 10 trials of initial baseline trials]). Next, we rotated the participant's visual scene with prism glasses. The glasses, which occluded the view of the body and throwing arm, caused participants to perceive the target offset by 30° in space from its true position. Past the target, balls disappeared underneath a black curtain, which along with black flooring, reduced spatial reference cues. In response, participants committed throwing errors (Fig. 2A, blue rotation period) which induced rapid adaptation; participants adjusted their movement angle to mitigate the discrepancy between ball and target, reaching asymptotic performance[19] by approximately their 13th trial with -1.29° error persisting over the last 3 trials of the period (Fig. 2A).

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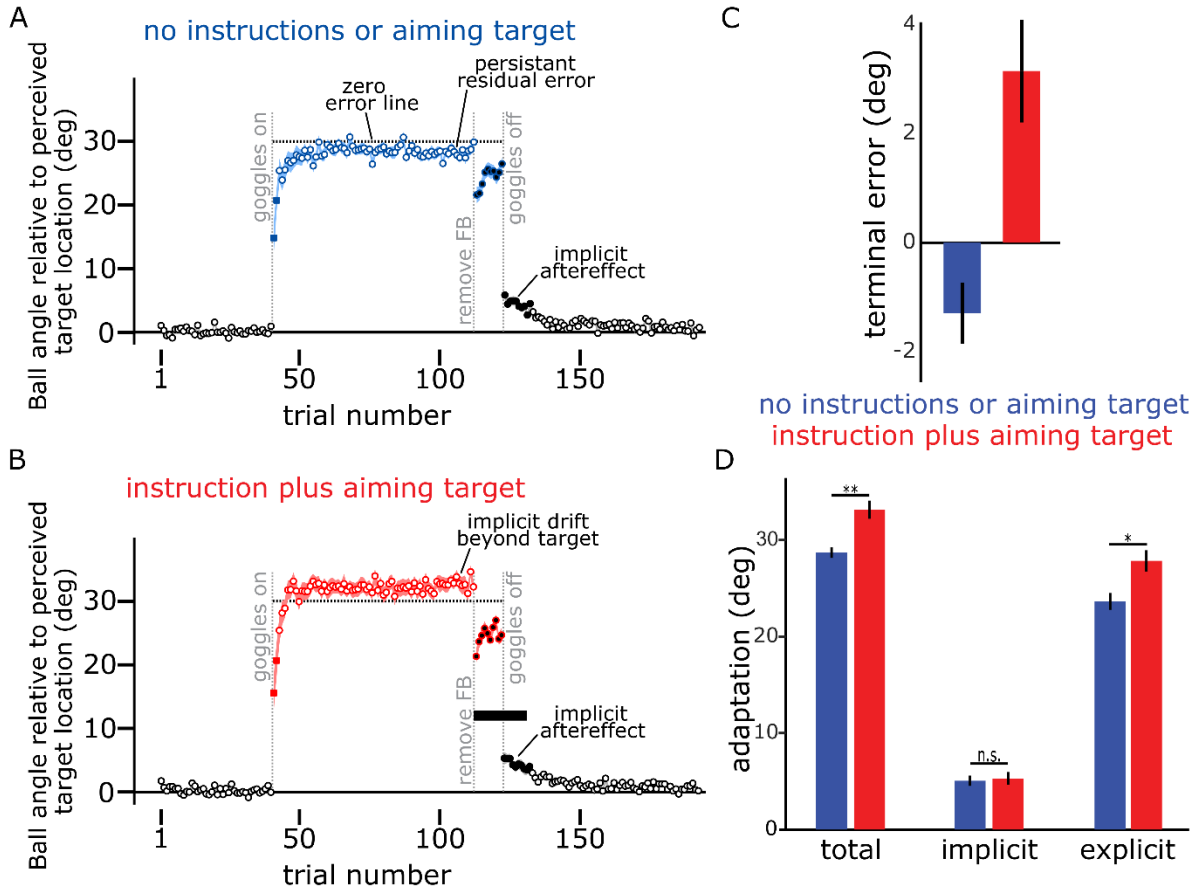

Figure 2. *Implicit and explicit components of unconstrained movements*. **A.** Trial-by-trial lateral error during ball rolling relative to the perceived target with no strategic instructions or aiming target provided (n = 27). Black-outlined datapoints represent trials with no visual shift applied. Blue-outlined points represent trials with a 30° visual shift applied. After the first two visually shifted trials (blue squares), participants were reminded of the goal to hit the target. Black-filled datapoints indicate the absence of visual endpoint error feedback. **B.** Trial-by-trial error for participants given an aiming target to minimize error (n = 27). Red-outlined datapoints indicate trials with a 30° visual shift applied. After the first two visually shifted trials (red squares), the aiming target was added and described. **C.** Mean residual error on the last three trials of the visual shift block drifted beyond the target for the strategy group (red bar). **D.** Statistically significant differences between instruction and no instruction groups in total adaptation and explicit adaptation. Error bars represent standard error and asterisks indicate results of Bonferroni-corrected p-values from paired t-tests [* p=0.012; ** p=0.0005].

Was this rapid motor adaptation solely dependent on explicit changes in throwing strategies, e.g., intended aiming angle, or was some adaptation due to subconscious implicit learning? To measure implicit and explicit learning components, we instructed participants to continue making throws over 20 trials, but without error feedback. On these trials, participants could view the initial target location, but the room was darkened once the ball left the hand. For the initial 10 no-feedback trials, the rotation was maintained. Then, participants switched to the unshifted glasses for an additional 10 no-feedback trials. For these trials, participants were told that the glasses had been

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switched, and that they should aim towards the initial target location. We gave these instructions to match the conditions used to measure implicit learning via aftereffect trials in modern VMR experiments[1,8,20]. Throwing angles decreased from 28.71° (relative to perceived target location) at the end of the adaptation period, to approximately 5.06° on the initial 3 unshifted no-feedback trials (Fig. 2A, implicit aftereffect). This immediate voluntary change in angle implied that participants had explicitly aimed about 23.7° away from the perceived visual target (explicit strategy was estimated by subtracting implicit learning from total adaptation during the shifted vision block). An additional 5° of subconscious implicit learning decayed after a return to unshifted vision, both in the absence of feedback (one sample Bonferroni-corrected t-test confirming the slope of error over these trials to be significantly different from zero, $t(26) = -1.54$, $p= 0.0097$) and over the ensuing washout period ($t(26)= -2.74$, $p < 0.0001$).

In sum, motor behavior in our task showed a clear correspondence to lab-based VMR studies: (1) Participants adapted to the rotation, achieving steady-state performance that never completely counteracted the rotation[3,8,21]. (2) Learning was supported by two parallel systems[2,7,11,12]: an explicit strategy that participants could willfully disengage, and an implicit correction that persisted despite the participant's conscious intentions. But which error sources had engaged the implicit learning system? Implicit learning could have been caused by SPEs (error between predicted and realized motion), task errors (error between ball and target)[1,3,10,16], or a model-free reinforcement of successful motor actions[22].

To test whether SPEs contributed to adaptation we tested a second group with a paradigm similar to Mazzoni and Krakauer (2006) (Fig. 2B). Here, after performing two ball rolls with rotated vision, participants were told they could aim towards an assistive target in order to move the ball to the desired goal target. Participants adopted this strategy quickly, reaching steady-state performance in about 10 trials (see Methods[19]). Remarkably however, despite rapidly achieving zero error (i.e., hitting the target's center), the ball angle gradually drifted over time, overcompensating for the imposed rotation. By the last 3 trials of the period, the ball's path deviated by 3.15° *beyond* the task-related target (Fig. 2C), exceeding on average the target's extent (radius = 0.425°, $t(26) = 2.89$, $p = 0.0077$, 95% CI lower bound = 1.21°). We confirmed a statistically significant main effect of the added instructions on this total adaptation with a multiple linear regression ($F(2,51) = 10.00$, $p = 0.00022$ for total adaptation response variable; $\beta_{Strategy} = 4.51$, $t(24) = 4.19$, $p = 0.00011$). This involuntary drift in reach angle is a distinct hallmark of implicit learning driven by SPEs. These experiments demonstrate that SPEs, a theoretical construct discovered in the laboratory, also lead to subconscious sensorimotor adaptation in skill-based tasks involving object manipulation.

Why did total adaptation increase when participants were provided an aiming target? Learning aftereffects observed immediately upon returning to unshifted vision, indicating implicit adaptation, did not show a statistically significant difference between groups (5.06° (no aiming target), 5.30° (aiming target) ($F(2,51) = 0.89$, $p = 0.42$ for implicit adaptation response variable). Since implicit adaptation does not explain the difference in total adaptation, the increase in total adaptation noted is explained by a difference in explicit strategy use (no aiming target: 23.64°; aiming target: 27.85°) ($t(52) = -3.00$, $p = 0.0123$; follow up paired t-test with Bonferroni correction, see Methods for details) (Fig. 2D).

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Explicit strategies also exhibited experience-dependent variation; that is, after participants completed the initial learning period, they were tested in the alternative experimental condition (Fig. 3), yielding order effects. First, we observed that drift past the task-related target tended to be greater when aiming targets were provided during the second learning period (4.31°, Fig. 3D) than the first learning period (2.06°, Fig. 3B) (not a statistically significant difference determined by an independent t-test: $t(25) = -1.20$, $p = 0.24$). This increased drift was likely due to increases in explicit strategy[23,24], which was saved upon reexposure to the same perturbation: the mean error on the first two shifted vision trials was significantly different on Block 1 (-19.36°, Fig. 3AB) compared to Block 2 (-4.71°, Fig. 3CD) as confirmed with a paired t-test ($t(26)=-8.09$, $p<0.0001$). A hybrid result was observed during the second adaptation period when no aiming target was provided (Fig. 3C). Savings in explicit strategy caused rapid elimination of residual error. Without an aiming target, residual error when presented in the second block (Fig 3C) tended to be reduced to -0.59° compared to -2.05° during first block sessions, though this difference was not statistically significant (Fig 3A, independent t-test: $t(25) = -1.33$, $p = 0.20$).

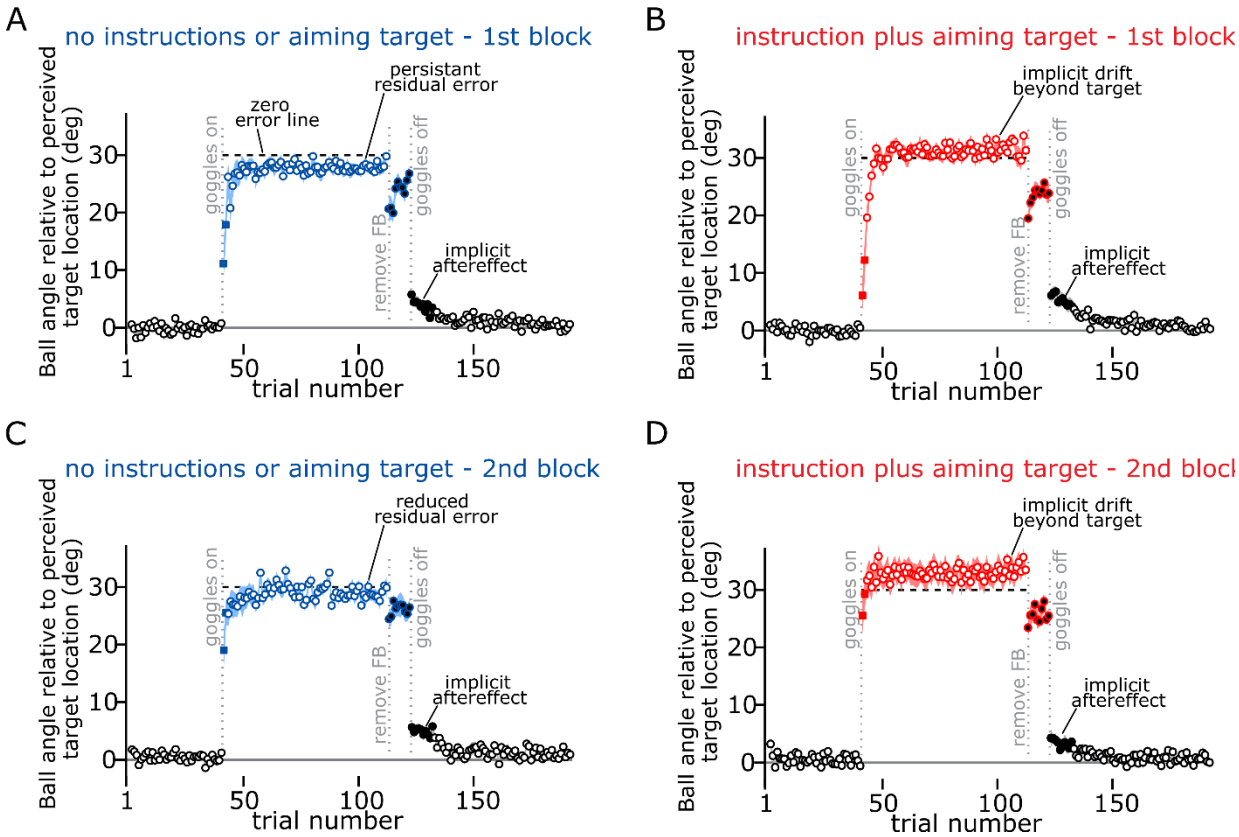

Figure 3. *Trial-by-trial error across all block order and strategy condition pairs.* **A.** Data plotted for participants completing their first block without an aiming target (n = 13). Plotting conventions as described in Figure 2. **B.** Data from Block 1 of participants using an aiming target (n = 14). **C.** Data from Block 2 of participants without an aiming target who first used an aiming target, the same participants as in panel B (n = 14). **D.** Data from Block 2 participants with an aiming target who first had no aiming target, the same participants as in panel A (n = 13).

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Discussion

Error-based motor adaptation has been studied extensively in controlled laboratory conditions, but little is known about whether this vast body of work applies to ecological skill-based behaviors. Here, we observed direct evidence that (1) subconscious error-driven learning processes make substantial contributions to skill-based motor adaptation, and (2) that this learning is in part mediated by SPEs not only in our body's motion, but in the motion of external objects that we impart through complex motor actions.

Admittedly, using prism glasses to shift the visual world is not naturalistic. These findings simply represent a step towards more rigorous study of implicit and explicit learning processes "in the wild". To this end, our study differs from past skill-based learning investigations[13–15], in notable ways. Most importantly, earlier reports[2,7,11,12,17], have inferred implicit (or procedural) adaptation, under the assumption that the aftereffect during the washout period is entirely driven by implicit processes. This is problematic, as there is no guarantee that participants will stop using explicit strategies, especially when errors are not removed during the washout period which can continue to guide aiming strategies.

Furthermore, there has been no attempt to delineate the potential error sources which could drive subconscious adaptation in a skill-based setting. That is, SPEs and target-errors always co-occur with one another (i.e., the discrepancy between the hand/object and target creates a task error, and a discrepancy between the hand/object and predicted path creates the SPE) and are both known to drive implicit adaptation[1,3,7,10,16]. On the other hand, implicit recalibration may occur through an error-free process such as reinforcement learning. That is, strategies could initially modulate the motor plan, and then be transferred to the implicit system through the development of a use-dependent bias[22,25]. In sum, special experimental conditions must be used to isolate adaptation that can only be attributed to SPEs, which have rarely been applied even in lab-based settings[1,2,7].

Here we solved both these issues by adopting the standard best practices in measuring the implicit contribution to adaptation: (1) instructing participants to not use strategy (i.e., aim directly to the target)[3,8,26], and (2) removing all visual feedback that could be used to inform them about the success of their movements[27,28] (in our case, by darkening the room during the no-aiming period). Second, to ensure that this implicit aftereffect was at least in part driven by SPEs, we provided a secondary aiming landmark[2,7] that helped participants eliminate the target error; adaptation beyond this point must be driven by an SPE, because there is no remaining discrepancy between the ball and the target.

The result was a clear implicit aftereffect that exhibited decay properties resembling those studied in lab-based settings. That is, even in the absence of error, the act of moving and the passage of time alone resulted in the partial loss of this memory trial-to-trial[1,27,29–32]. Further, we could attribute this implicit aftereffect at least in part to SPEs due to the counterintuitive drift beyond the primary target (Fig. 2B, implicit drift beyond the target). It is rather remarkable that this distinct SPE-driven phenotype is preserved across motor actions with stark differences in complexity; Mazzoni and Krakauer (2006) studied the movement of an index finger with their arm immobilized via splinting to a tripod, whereas the ball's path in our task was due to a complicated whole-body coordination that imparted motion on a physical object. In our view, this speaks to the strength and ubiquity of SPE-learning, which we speculate fine tunes our motor behaviors in everyday life.

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There are, however, some differences in the magnitude of this aftereffect between our study and past lab-based investigations. Importantly, the 5° implicit aftereffect we detected was smaller than that observed in past studies, which reached 20-30°. While we can only speculate as to the cause, one important possibility is temporal delay; given the ~20 ft displacement between participant and target in our task, the ball arrived approximately 0.75 sec after the participant completed their motor action. These conditions are known to attenuate implicit learning[8,17,18], likely due to misalignment between motor and error signals in the cerebellar cortex[33–35].

It is also interesting to note that our skill-based implicit aftereffect did not appear to differ in magnitude whether the secondary aiming target was provided or omitted (Fig. 2D). This is opposite to Mazzoni and Krakauer (2006), who observed an elevated aftereffect in conditions in which no strategy is given[2]. Target errors may contribute to this apparent discrepancy. When no strategy is given, learning occurs slowly leading to a large target error[1,3,7,10,16] that can combine with SPEs to drive implicit learning[3]. Indeed, in Mazzoni and Krakauer (2006), learning occurred slowly when no secondary target was provided (Fig. 4B, no drift group), leading to sustained target errors that were at least 10° or larger throughout the adaptation period. On the other hand, even when a secondary aim target was not given, learning in our task was rapid, reducing the target error to only about 2° within 10 trials or so (Fig. 4A, no aim target). This rapid learning was likely due to strategy use, which was high in our task, about 25° (80% of the total perturbation size). We hypothesize that large explicit strategies deprived the implicit system of target errors, a learning substrate that would have enhanced the implicit aftereffect. These ideas could be further investigated in future studies by reducing explicit strategies (thus keeping target errors large) by adding more training targets[36], or limiting movement preparation time[3,8,24,26,37,38].

The importance of the target error in strengthening, or adding to, an SPE is also implied by the absence of drift in the no aiming target condition. That is, no drift beyond the target was evident at any point during the training period, despite rapidly reducing total error to 2° and the continued presence of an SPE between the ball's path and its predicted trajectory. This strongly indicates that SPEs need to be reinforced by a visual target error in order to drive appreciable implicit learning; this pattern also matches that observed in constrained laboratory settings[2,7] when Taylor and Ivry (2011) trained participants to aim without an assistive aiming target (Fig. 4C, no drift). Moreover, when these authors measured the implicit aftereffect, they observed a substantial attenuation when an aiming target was not present or removed partly through the reaching movement. This is all to suggest that SPEs do not operate alone but are reinforced by visual target errors. We speculate that this applies to both lab-based and skill-based settings, though the latter requires substantial follow-up investigation.

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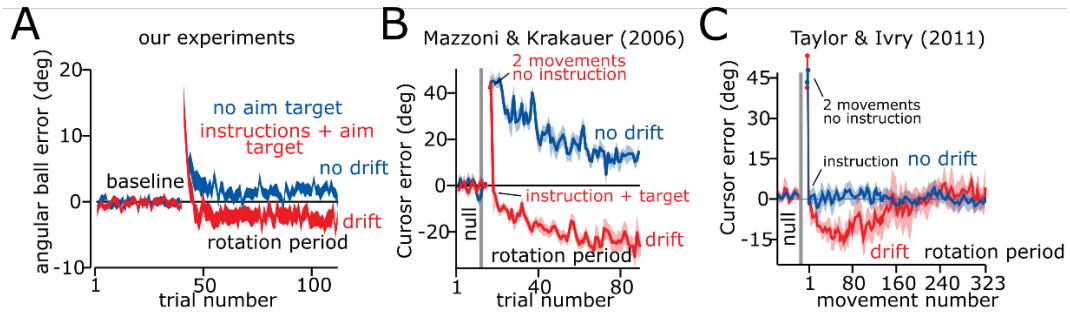

Figure 4. *Implicit drift occurs in several experimental contexts.* **A.** Trial-by-trial error data from Figure 2AB with actual target error appearing on the y-axis. Providing an aiming target (in red) caused the angular ball error to drift beyond the target (i.e., past zero), thus overcompensating for the visual rotation. **B.** Results from Mazzoni and Krakauer (2006), an analogous lab-based experiment, which have been widely cited as evidence for SPE learning. Participants were either given no instruction (blue) or were instructed to use an aiming target to "solve" the rotation and reduce error (red). **C.** Results from Taylor & Ivry (2011), a modified version of the experiment from B. Participants were either given an aiming target (red) or taught how to re-aim their movement to counter the rotation without an additional target (blue). Even with an explicit strategy, there is no drift beyond the target in the absence of an aiming target (blue).

Another possible force that attenuates potential drift is a change in explicit strategy. That is, aim reporting protocols have demonstrated late reductions in explicit strategy during training, which presumably functions to prevent the overcompensation that can result from continued SPE-driven implicit learning[11,12]. Similarly, Taylor and Ivry (2011) demonstrated that drift beyond the target is eventually eliminated with sufficiently long exposure to the rotation (Fig. 4C, drift group). Future studies with a longer perturbation block would be required to detect this strategic phenotype in our skill-based task. Indeed, this phenomenon was hinted in the order effects displayed in Fig. 3; when participants transition from the aim target condition, to the no-aim target condition, target error was reduced to 0°, followed by what appeared to be a slight decline in total adaptation (Fig. 3C). This decline could have been driven by a voluntary reduction in strategy.

In sum, our work implicates implicit SPE-driven adaptation in skill-based settings and represents an initial step towards interrogating how implicit learning helps to counter perturbations that humans encounter as they execute common motor skills. Substantial work remains to better elucidate how this implicit learning can be strengthened or attenuated, e.g., via target errors, and how implicit processes are coordinated with explicit strategy. Further, motion capture must be applied to more deeply investigate whether markers of implicit and explicit adaptation can be differentiated across distinct movement components (e.g., trunk orientation and release timing may reflect strategy, whereas wrist and elbow joint angles may be controlled by an implicit process).

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Methods

Ethics statement. Human participant research was completed with the approval and oversight of the Rhodes College Institutional Review Board.

Subject recruitment. Thirty study participants were recruited by word of mouth, and each given a $10 gift card for their participation (mean age = 20yrs; age range – 18 – 21; 21 female; 29 right handed but all completed ball throws with right). Data from three participants were omitted because of technical issues that resulted in missing video files that contained motor error data. Written informed consent was obtained from each participant before completing the experiment.

Experimental setup. Participants stood behind a line marked on the floor facing a small target (D=0.85°) on the ground 6.1m away. They were informed about the task parameters: to use an underhand motion to roll a tennis ball so that it moved through the target. The experiment took place in a black box theater with black flooring and a black curtain behind the target area under which balls rolled out of view. Participants started by wearing goggles with clear lenses that allowed for unperturbed vision (Fork in the Road Vision Rehabilitation Services LLC, Madison, WI). During shifted vision blocks, participants wore Perception (Distortion) goggles (WinginItProducts, Pleasant Prairie, WI) that caused the participants to perceive visual targets offset in space by 30° from their true position. Both types of goggles occluded the view of the body and throwing arm and participants were asked to release the tennis ball below their waist level so the hand was never visible.

An infrared video camera (Prime Color, Optitrack) was mounted directly above the target (~7 meters above attached to a theater lighting grid). The camera was pointed at the target, capturing several meters of linear space on both sides of the target. It recorded the tennis ball rolling along the floor so that rolling error could be computed (see Data analysis). The camera was attached to a computer which displayed and recorded the video in Motive software (Optitrack). A single eStrobe (Optitrack) mounted above the target (next to the camera) provided the only illumination in the room and could be toggled on and off with a single button press in the Motive software.

A researcher kneeled next to the participant and handed tennis balls to the participant for each subsequent roll. Another researcher stood behind the curtain and collected tennis balls to make sure they did not roll back onto the visible floor space. A third researcher monitored the video recording and controlled the lights during no feedback trials. For some participants, only two researchers were present and the tennis ball wrangling and computer monitoring were done by the same individual.

Data collection. Each participant completed two blocks of 192 tennis ball rolls. In the 'No Instructions' block, participants were not given a strategy to counteract the visual perturbation. In the 'Aiming Target' block, participants were given a secondary target to use that would minimize the error resulting from the visual perturbation. The order of the blocks was randomly assigned to the participants (after the three excluded participants, 13 participants completed 'No Instructions' first and 14 participants completed 'Aiming Target' first).

Participants first completed 40 baseline movement trials, rolling the ball to the target without shifted vision. Then participants switched to goggles that shifted their vision by 30°. To switch the

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goggles, participants first closed their eyes. The researcher then assisted with doffing the current goggles and donning the new goggles. With eyes still closed, participants were then guided through a series of in-place rotations in order to reset the relative orientation between the target and the body. Then participants opened their eyes.

In the 'No Instructions' block, participants then completed two trials with shifted vision after which the researcher said: "Try to hit the target.". Participants then completed another 70 trials with the shifted visual feedback.

In the 'Aiming Target' block, participants completed two trials with shifted vision after which the researcher placed an aiming target, matching the size and appearance of the original target, 30° to the right of the original target. The researcher then explained to the participant: "You just made two large errors because we imposed a rotation that pushes you 30 degrees to the left. You can reduce this error by aiming at the new target to your right."

After 72 total trials with the shifted goggles, participants then completed 10 trials with the same visual shift but with no endpoint error feedback. Participants were made aware before these trials that the light would turn off immediately after they released the ball. The researcher controlling the computer manually shut off the eStrobe light as soon as the tennis ball first hit the floor at the start of the participant's roll, making the room completely dark. Since the camera was imaging in the infrared spectrum, the tennis ball could still be viewed from the computer. As soon as the tennis ball passed the target and went out of view underneath the curtain, the researcher turned on the light.

After 10 trials with no endpoint visual feedback, the goggles were switched back to the clear lens goggles and participants were told: "I would like you to aim for the original target again." Participants completed 10 additional trials without endpoint visual feedback with no vision shift. Then participants completed 60 trials with no visual shift with endpoint visual feedback (i.e. the lights stayed on).

Data analysis. Video recordings were analyzed using Vernier Video Analysis software (Vernier Science Education, Beaverton, OR). Small pieces of tape on the ground set at 1m apart and visible in the video frame but not visible to participants were used to calibrate position measurements in the software. When the tennis ball was in line with the target, its position was marked manually with a mouse click in the software for each trial. The lateral error between the target and tennis ball was computed for the entire set of trials using the marked positions on the video frames.

Data were loaded into MATLAB software and a custom script was used to calculate descriptive statistics and identify the steady-state trials during the visual rotation block after which learning had stabilized[19]. Total Adaptation was calculated as the sum of the visual shift (30°) and the mean error over the last three trials of the shifted vision with feedback trials [i.e. how much movements were adapted under the visual shift]. Implicit adaptation was calculated as the mean error over the first three trials immediately after switching to unshifted vision (after the shifted vision block). Explicit adaptation was computed as the difference between Total Adaptation and Implicit Adaptation. Graphical plots were generated in R and MATLAB supported by publicly available scripts[39,40].

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A multiple linear regression was run in RStudio (v2022.07.1, R version 4.1.1) with Total Adaptation and Implicit Adaptation as the outcome variables and Block Number and Strategy Condition (i.e. with or without aiming target) as the predictor variables. Explicit Adaptation was not included in the regression since it is computed from the included outcome variables and thus correlated with them. Secondary inferential statistical analyses were conducted to further explain the results. Bonferroni-corrected p-values from t-tests were used to describe pairwise comparisons that appear in Fig 2CD. The same analysis was run on pairwise comparisons with data separated into the four different blocks (Fig. 3). The mean tennis ball error during the last three trials of the rotated vision trials with feedback was analyzed using a one sample t-test to determine if the ball's error was beyond the physical extent of the target (i.e. including the radius of the target and ball). To investigate savings (and by extension, the influence of an explicit strategy), a paired t-test was run comparing initial error on the first two visual shift trials between Block 1 and Block 2.

Data and code. All data, analysis code and plotting scripts are available here: https://osf.io/8kf59/?view_only=cfeb2f109d304994bbd3a5f5a44c11ae

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