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Title: Task errors contribute to implicit aftereffects in sensorimotor adaptation

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### Abstract

Perturbations of sensory feedback evoke sensory prediction errors (discrepancies between predicted and actual sensory outcomes of movements), and reward prediction errors (discrepancies between predicted rewards and actual rewards). When our task is to hit a target, we expect to succeed in hitting the target, and so we experience a reward prediction error if the perturbation causes us to miss it. These discrepancies between intended task outcomes and actual task outcomes, termed “task errors”, are thought to drive the use of strategic processes to restore success, although their role is incompletely understood. Here, as participants adapted to a 30° rotation of cursor feedback representing hand position, we investigated the role of task errors in sensorimotor adaptation: during target-reaching, we either removed task errors by moving the target mid-movement to align with cursor feedback of hand position, or enforced task error by moving the target away from the cursor feedback of hand position, by 20-30° randomly, clockwise in half the trials, counterclockwise in half the trials). Removing task errors not only reduced the extent of adaptation during exposure to

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the perturbation, but also reduced the amount of post-adaptation aftereffects that persisted despite explicit knowledge of the perturbation removal. Hence, task errors contribute to implicit adaptation resulting from sensory prediction errors. This suggests that the system which predicts the sensory consequences of actions via exposure to sensory prediction errors is also sensitive to reward prediction errors.

### Introduction

Successful goal-directed movement requires the capacity to adapt movements to unexpected changes in the properties of our world or our moving bodies. Such changes are thought to evoke sensory prediction errors, or discrepancies between predicted sensory outcomes and actual sensory outcomes of our movements (c.f., Jordan & Rumelhart, 1992). Sensory prediction errors are thought to drive a remapping of the relationship between motor commands and the predicted sensory outcomes of motor commands (e.g., Izawa & Shadmehr, 2011). Perturbations also elicit an unexpected failure to attain the reward of hitting the target (i.e., a negative reward prediction error) (Izawa & Shadmehr, 2011). It is clear that behavioural responses to perturbations are affected not only by sensory prediction errors, but also by reward prediction errors (Izawa & Shadmehr, 2011; Cashaback *et al.*, 2017; Palidis *et al.*, 2018). However, how reward prediction errors and rewards affect sensorimotor adaptation is not fully understood. Mounting evidence shows that extrinsic rewards such as gaining or losing pleasing feedback, points, money, or food can modulate sensorimotor adaptation (e.g., Madelain *et al.*, 2011; Galea *et al.*, 2015; Nikooyan & Ahmed, 2015; Gajda *et al.*, 2016; van der Kooij & Overvliet, 2016; Kojima & Soetedjo, 2017; Quattrocchi *et al.*, 2017; Song & Smiley-Oyen, 2017), but less is known about how adaptation is affected by intrinsic rewards associated with accomplishing task goals (Widmer *et al.*, 2016; Kim *et al.*, 2017b).

The unexpected failure to attain the task goal of hitting the target, or task errors, are thought to drive the use of explicit compensatory strategies (Taylor & Ivry, 2011), such as re-aiming to one side of a target when visual feedback of the moving limb is laterally perturbed (Welch, 1969). This explicit learning is thought to be flexible: it can be volitionally disengaged when no longer useful (McDougle *et al.*, 2016). In contrast, sensory prediction errors triggers a form of learning that is less easy to disengage, and is thought to occur in an implicit fashion (Mazzoni & Krakauer, 2006). Although adaptive behaviour to compensate for perturbations can be driven by sensory prediction errors or reward prediction errors (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015; Cashaback *et al.*, 2017; Palidis *et al.*, 2018), it has been suggested that only sensory prediction errors can produce a change in the system that predicts sensory consequences of motor commands: reward prediction errors alone are insufficient (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015). However, because these studies never made both sensory prediction errors and reward prediction errors concurrently available in the same conditions, it remains unclear whether reward prediction errors modulate implicit adaptation to sensory prediction errors.

Here, we tested whether reward prediction errors contribute to implicit adaptation to sensory prediction errors. During typical sensorimotor adaptation paradigms where the task is to move to the target, we assume that success or failure in moving to the target (i.e., task errors) is an intrinsic reward signal. In this experiment, when participants were exposed to a 30° rotation of cursor feedback that represented their hand position, we either (1) removed task error by shifting the target mid-movement to align with the (measured) initial cursor direction, such that the cursor always hit the target, (2) enforced task error by shifting the target away from the cursor by mid-movement between 20 to 30° randomly (clockwise in half the trials, counterclockwise in half the trials), such that the cursor never hit the target, or (3) allowed standard task error by maintaining a constant target position during the trial. Removing task error dramatically reduced the extent of error compensation to the cursor rotation, but also reduced the amount of implicit adaptation

resulting from exposure to sensory prediction errors. Enforcing task errors resulted in slower error compensation than the standard task error condition, but did not alter the amount of post-adaptation implicit adaptation compared to the standard task error condition. These results suggest that the reward prediction error of hitting or missing targets contributes to the formation of altered sensorimotor maps that result from exposure to sensory prediction errors.

## Methods and Materials

### Participants

There were a total of 142 participants (38 male, age range 17-59 years, mean age 21.3+/-0.4). All participants were naïve to visuomotor rotation and force-field adaptation tasks, and were naïve to the aims of the study. Participants received course credit or monetary reimbursement upon study completion. The study was approved by the Human Research Ethics Committee at The University of Queensland. All participants provided written informed consent. This study conforms with the Declaration of Helsinki.

### Apparatus

Participants completed the task using the vBOT planar robotic manipulandum, which has a low-mass, two-link carbon fibre arm and measures position with optical encoders sampled at 1,000 Hz (Howard *et al.*, 2009). Participants were seated on a height-adjustable chair at their ideal height for viewing the screen for the duration of the experiment. Visual feedback was presented on a horizontal plane on a 27" LCD computer monitor (ASUS, VG278H, set at 60Hz refresh rate) mounted above the vBOT and projected to the participant via a mirror in a darkened room, preventing direct vision of her/his hand. The mirror allowed the visual feedback of the target (a 0.5 cm radius yellow circle), the start (a 0.5 cm radius white circle), and hand cursor (0.5 cm red radius) to be presented in the plane of movement, with a black background. The start was aligned approximately 10cm to the right of the participant's mid-sagittal plane at approximately mid-sternum level. An air-sled was used to support the weight of participants' right forearms, to minimize possible effects of fatigue.

### General Trial Structure

Participants made centre-out reaching movements towards targets while grasping the robot arm. Targets appeared in random order at one of eight locations at a radius of 9 cm from a central start circle. The target locations were distributed uniformly throughout 360° (0°, 45°.... 315°). At the start of each trial, the central start circle was displayed. If participants failed to move the hand to within 1cm of the start circle after 1 second, the robotic manipulandum passively moved the participant's hand to the start circle (using a simulated 2 dimensional spring with the spring constant magnitude increasing linearly over time). A trial was initiated when the cursor remained within the home location at a speed below 0.1cm/s for 200ms. We used a classical timed-response paradigm (e.g., Schouten & Bekker, 1967) to manipulate movement preparation time during the planar reaching task (Favilla & De Cecco, 1996). Across all conditions, a sequence of three tones, spaced 500ms apart, was presented at a clearly audible volume via external speakers. Participants were instructed to time the onset of their movements with the onset of the third tone, which was more highly-pitched than the two previous, and slice through the target with their cursor. Movement initiation time was identified online as when hand speed exceeded 2cm/s. Targets appeared at 1000ms minus a display latency ( $27.6 \pm 1.8$ ms), before the third tone. Thus, target direction information became available 972ms before the desired initiation time. When movements were initiated 50ms later than

the third tone, the trial was aborted: the screen went black and the text “Too Late” was displayed on the feedback screen. When movements were initiated more than 100ms before the desired initiation time, the trial was aborted: the screen went black and a “Too Soon” error message was displayed. Thus, movements had to be initiated between 872 and 1022ms of target presentation. We chose this movement preparation time for consistency with our previous work using the timed-response paradigm with visuomotor rotations (Leow *et al.*, 2016). No visual feedback about movements was available when trials were aborted, and so such trials were immediately repeated. We enforced long movement preparation times across all conditions to prevent the possibility that the task error manipulation resulted in self-selection of different movement preparation times. All groups thus had ample opportunity (ample amount of time for movement preparation) to use explicit strategies.

To familiarize participants with the timed-response paradigm, all participants were first allowed a familiarization block of a maximum of 6 cycles (48 trials, where 1 cycle was 1 trial to each of the 8 targets, and target order was random within each cycle). Participants were explicitly instructed to make shooting movements through the targets, rather than to stop on the targets. Cursor feedback terminated as soon as the desired movement extent (the 9cm distance between the start and the target) was achieved. Subsequently, all participants (regardless of assigned condition) were given the same task instruction, as follows. “Your task in this experiment is to hit the targets. The computer might disturb the cursor and/or the target, this is a normal part of the experiment, just try to hit the target as well as you can”. Participants then completed the following blocks, where 1 cycle contained 1 trial to each of the 8 targets (target order was random within each cycle). Baseline (6 cycles): no rotation of visual feedback. Adaptation (60 cycles): A 30° rotation of cursor feedback representing the hand position was imposed. Half of all participants encountered a clockwise 30° rotation and half encountered a 30° counterclockwise rotation. 30° rotation of visual feedback. No feedback (6 cycles): Upon leaving the start circle, no feedback about movements were available. Before this block, participants received explicit instructions about the rotation removal, as follows: “Any disturbance that the computer has applied is now gone, and the feedback of your movement will now be hidden after it leaves the start circle, so please move straight to the target”. Between each block, there was a small delay to allow loading of the computer code for different experimental blocks and/or experimental instructions.

During the adaptation block, task errors were manipulated in three conditions. In the StandardTaskError condition, the target remained stationary throughout the trial, such that whether or not the perturbation evoked a task error was contingent on the participant’s reach direction (figure 1 top panel). Task errors were removed in the NoTaskError condition by moving the target to align with the direction of cursor velocity when the hand had moved 4cm (of the 9cm distance) from the start position (see figure 1 middle panel). This is analogous to moving a basketball hoop towards the ball mid-flight; the ball always goes through the hoop regardless of the person’s actions. Finally, in the EnforcedTaskError condition, task errors were enforced on every trial regardless of reach behaviour; the target was shifted randomly by 20° to 30° (counterclockwise in half the trials, clockwise in half the trials) relative to the cursor direction when the hand had moved 4cm from the start (see figure 1 bottom panel). This is analogous to moving a basketball hoop away from the ball’s trajectory; participants can never get the ball through the hoop regardless of where they shoot. Note, however, that in this condition, because the target jumped 20-30° counterclockwise from the cursor direction in half of the trials, and 20-30° clockwise from the cursor direction in the other half of the trials, when faced with a 30° cursor rotation, the target would move only minimally (0-10°) in approximately half the trials during early adaptation. In these trials, the task conditions are similar to those experienced in standard conditions where the targets do not jump. Across all conditions, cursor feedback was displayed after the hand had moved 4cm from the origin (i.e., the point at which cursor direction was measured to define potential target shifts).

Figure 1. Experimental conditions. StandardTaskError (top panel): target remained stationary within a trial. NoTaskErrors (middle panel): target shifted mid-movement (i.e., when the cursor had moved 4cm out of the 9cm start to target distance) to align with on-screen cursor direction, such that the cursor always hit the target. EnforcedTaskErrors (bottom panel): target shifted mid-movement away from on-screen cursor direction, randomly by 20 to 30° (clockwise in approximately 50% of the trials, and counterclockwise in approximately 50% of trials), such that the cursor could not hit the target.

For the main experiment (Experiment 1), we ran three participant groups (one for each of the three experimental conditions: StandardTaskErrors,  $n=30$ , 23 female, mean age 20.5, range: 17-34 years, NoTaskErrors,  $n=32$ , 19 female, mean age 21, range 17-39, and EnforcedTaskErrors,  $n=32$ , 23 female, mean age 21.4, range 18-33). Due to experimenter error, five of the 30 participants in the StandardTaskError group completed 1 no-feedback cycle instead of 6 no-feedback cycles. We also ran a follow-up study (Experiment 2) with 30 instead of 60 adaptation cycles, with three participant groups (StandardTaskError,  $n=16$ , age 18-22, 11 female; NoTaskError,  $n=16$ , age 18-30, 10 female, EnforcedTaskErrors,  $n=16$ , age 17-59, all female).

### Data analysis

Movement onset time was taken as the time at which hand speed first exceeded 2 cm/s. Reach directions were quantified at 20 percent of the radial distance between the start and the target. This procedure ensured that movement direction was quantified at less than 200ms into the movement, at which time the size of online corrections in hand position is small. Reaches with absolute initial direction errors greater than 60° with respect to the target (movements that were more than 60° to the left or the right of the target) were considered outliers, and were removed from analyses (Experiment 1: EnforcedTaskError, 0.66%, NoTaskError, 0.38%, StandardTaskError, 0.64%; Experiment 2: EnforcedTaskError, 0.51%, NoTaskError, 0.06%, StandardTaskError, 0.08%). Excluding these trials did not have any qualitative impact on the results. Trials were averaged in cycles of eight (one trial for each target angle) for statistical analysis. Reach direction errors for participants who experienced clockwise rotations (+30°) were sign-transformed for combined analysis with data for participants who experienced counter-clockwise (-30°) rotations.

Intrinsic biases in reaching direction can affect adaptation (Ghilardi *et al.*, 1995; Vindras & Viviani, 1998; Morehead & Ivry, 2015). Intrinsic biases were evident in the baseline block, as reaches deviated significantly from 0 in the last baseline cycle ( $p = .001$ ). To estimate intrinsic biases, we averaged reach directions from baseline cycles 2 to 6, and then subtracted this value from all cycles in all adaptation, no-feedback, and washout cycles, similar to previous work (Leow *et al.*, 2017). All subsequent analyses were run on bias-corrected reach directions.

We tested how the different task error conditions altered the time-course of adaptation by running mixed ANOVAs with the within-subjects factor Cycle (reflecting changes in reach direction across increasing cycles) and the between-subjects factor TaskError (StandardTaskErrors, EnforcedTaskErrors, and NoTaskErrors) for the first 30 adaptation cycles. Partial eta-squares were used to report ANOVA effect sizes, with values in excess of 0.14 considered large. When Mauchly's test of sphericity was statistically significant, the Greenhouse-Geisser correction was used to adjust degrees of freedom.

To test the completeness of adaptation, we estimated adaptation extent by taking the mean of the last 5 cycles of the adaptation block. Disengagement of explicit learning after notification of the perturbation removal was estimated as the difference between the first no-feedback cycle and the last adaptation cycle. The size of implicit aftereffects, which reflects an altered map between motor commands and its predicted sensory outcomes, were estimated as the mean of the first no-feedback cycle after notification of the perturbation removal. Note that we did not additionally quantify the decay of implicit aftereffects, because our experiment, with only 6 no-feedback cycles in Experiment 1, was not optimized to measure this. The decay of the aftereffect might reflect persistence of this learning, and is influenced by many factors, such as the adaptation schedule (Hamilton & Bossom, 1964; Hatada *et al.*, 2006; Joiner & Smith, 2008; Huang & Shadmehr, 2009; Vaswani & Shadmehr,

2013), and might be mechanistically distinct from the size of the aftereffect. We thus limited our analyses to the size of the aftereffect measured only in the first no-feedback cycle, similar to previous work (Taylor et al., 2014; Bond & Taylor, 2015; Brudner et al., 2016; Morehead et al., 2017). To test if these measures differed between experimental conditions, we used ANOVAs with within-subjects factor Task Error (StandardTaskError, EnforcedTaskError, NoTaskError) and follow-up t-tests and Cohen's *d* to estimate effect sizes when Shapiro-Wilk tests showed no violations of normality. Cohen's *d* values of .8, .5, and .2 represented large, medium, and small effect sizes. When Shapiro-Wilk tests showed violations of normality, we used Kruskal-Wallis tests, followed by Mann-Whitney U-tests, with effect sizes quantified as *r*, where *r* is *z* divided by the square root of the number of observations (Fritz et al., 2012). For *r*, a large effect is .5, a medium effect is .3, and a small effect is .1 (Fritz et al., 2012). Bonferroni corrections were applied in the cases of multiple comparisons. Only two-sided tests were used. An alpha level of .05 was used. Statistical analyses were performed with JASP (Version 0.8.5) and SPSS. Graphs were plotted with GraphPad Prism version 7.00 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com.

## Results

### Removing task error reduced error compensation

We examined how manipulating task errors altered how people adapted reaching movements to sensory prediction errors evoked by rotating cursor feedback of hand position. Before encountering the cursor rotation, participants showed a counterclockwise reach bias, although this bias did not differ reliably between groups. Fig 2a shows bias-corrected and cycle-averaged movement directions for each task error condition. Values closer to the ideally adapted movement direction (30°) indicate more complete compensation for the cursor rotation.

**Adaptation (cycles 1 to 30):** In the first 30 adaptation cycles, reaches were least adapted with NoTaskErrors (12.5+/-1.2°), followed by EnforcedTaskErrors (14.3+/-0.9°), and most adapted with StandardTaskErrors (24.2+/-0.8°). Cycle x TaskError ANOVA showed a significant main effect of TaskError,  $F_{2,91} = 36.26$ ,  $p < 0.001$ , partial  $\eta$ -squared = 0.44, and a Cycle x TaskError interaction,  $F_{11.7, 534.4} = 3.06$ ,  $p < 0.001$ , partial  $\eta$ -squared = 0.06. Post-hoc comparisons showed that both the NoTaskError group and the EnforcedTaskError group showed less error compensation compared to StandardTaskErrors (both  $p < .001$ ). Adaptation in the NoTaskError and EnforcedTaskError groups did not differ reliably ( $p = .64$ ).

**Adaptation extent (cycles 56 to 60):** To evaluate the extent of adaptation to the perturbation, we compared the mean reach direction in the final 5 cycles (i.e., after more than 400 trials of exposure to the perturbation, fig 2b). The difference between task error conditions remained evident here. The EnforcedTaskError and NoTaskError group were not normally distributed due to one outlier in each group (see fig2b). A Kruskal-Wallis test showed a difference in adaptation extent between conditions,  $chi-square = 12.7$ ,  $p < .001$ . Adaptation was least complete with NoTaskErrors (18.2+/-1.7°), followed by EnforcedTaskErrors (22.7+/-1.4°) and StandardTaskErrors (29.7+/-0.6°). StandardTaskErrors resulted in more complete adaptation compared to NoTaskErrors,  $U = 77$ ,  $z = 5.677$ ,  $p < 0.001$ ,  $r = 0.77$ , large effect size. Adaptation was less complete with NoTaskErrors compared to EnforcedTaskErrors,  $U = 95$ ,  $z = 5.423$ ,  $p < 0.001$ ,  $r = 0.6$ , large effect size. NoTaskErrors resulted in less complete adaptation to the perturbation than EnforcedTaskErrors,  $U = 298$ ,  $z = 2.873$ ,  $p = 0.004$ ,  $r = 0.36$ , medium effect size.

Figure 2a. Group mean $\pm$ -SEM for reach directions across all cycles (1 cycle=8 trials=1 visit to each of the 8 targets). Reaches closer to 30° represent more complete error reduction. Adaptation was least complete with NoTaskErrors (red), followed by EnforcedTaskErrors (blue) and StandardTaskErrors (green). 2b. Asymptote (mean reach direction in the last 5 adaptation cycles). 2c. Implicit aftereffects (mean reach direction in the first no-feedback cycle). Implicit aftereffects in the NoTaskError group was reduced compared to the StandardTaskError group and the EnforcedTaskError group. 2d. Volitional disengagement of explicit learning, as quantified by the change in reach direction upon notification that the cursor rotation had been removed. 2e. Group mean $\pm$ -SEM for reach directions across all cycles for the follow-up experiment with 30 instead of 60 adaptation cycles. 2f. Adaptation extent, quantified in the last 5 of the 30 adaptation cycles. 2g. Less implicit aftereffects was evident with NoTaskErrors than with StandardTaskErrors. 2h. The NoTaskError group also did not show volitional disengagement of explicit learning. Error bars were standard errors of the mean for cycle by cycle data in 2a and 2e. Error bars were 95% confidence intervals for 2b-d and 2f-h.

### Disengagement of explicit learning:

Before the first no-feedback cycle, participants were explicitly told that the cursor rotation had been removed: this typically evokes a volitional disengagement of explicit learning, as evident in a change in reach direction between the last adaptation cycle compared to the first no-feedback cycle (Heuer & Hegele, 2008b; a; Hegele & Heuer, 2010). This change in reach direction is plotted in fig 2d. We quantified this volitional disengagement of explicit learning across the different conditions by comparing the last adaptation cycle to the first no-feedback cycle, using a TaskError x Cycle (last adaptation cycle, first no-feedback cycle) ANOVA. There was a significant TaskError x Cycle interaction,  $F_{2,91} = 9.69$ ,  $p < 0.001$ , partial  $\eta$ -squared = 0.17. Post-hoc paired t-tests comparing the last adaptation cycle to the first no-feedback cycle shows volitional disengagement of explicit learning with StandardTaskErrors,  $t_{29} = 6.46$ ,  $p < 0.001$ ,  $d = 1.18$ , but not with EnforcedTaskErrors,  $t_{31} = 0.78$ ,  $p = 0.44$ ,  $d = 0.13$ , and not with NoTaskErrors,  $t_{31} = -1.21$ ,  $p = 0.23$ ,  $d = 0.21$ . The finding that reaches did not differ reliably between the last adaptation cycle and the first no-feedback cycle despite explicit knowledge of the rotation removal for EnforcedTaskErrors and NoTaskErrors implies that these manipulations of task errors are a reasonable assay of implicit learning during exposure to the perturbation.

### Removing task error reduced implicit aftereffects

Implicit aftereffects: Implicit aftereffects were quantified by the extent to which reach direction remained adapted in the first no-feedback cycle despite explicit knowledge of rotation removal (Hegele & Heuer, 2010). Implicit aftereffects were only assessed via the first no-feedback cycle, as sensorimotor adaptation decays rapidly in the absence of feedback, even with explicit knowledge that the perturbation has been removed (Hamilton & Bossom, 1964; Taylor et al., 2014; Morehead et al., 2017).

Figure 2c shows smaller implicit aftereffects with NoTaskErrors,  $18.0 \pm 1.2^\circ$ , than StandardTaskErrors,  $22.1 \pm 1.0^\circ$ ,  $t_{59} = 2.63$ ,  $p = .01$ , cohen's  $d = 0.67$ , medium effect size. Implicit aftereffects were also reduced with NoTaskErrors,  $18.0 \pm 1.2^\circ$ , compared to EnforcedTaskErrors,  $21.6 \pm 0.8$ ,  $t_{53.8} = 2.56$ ,  $p = .013$ , cohen's  $d = 0.64$ , medium effect size. Hence, the absence of task failure in the NoTaskError condition resulted in both less adapted reaches and less post-adaptation implicit aftereffects than the constant presence of task failure in the EnforcedTaskError condition. Implicit aftereffects did not differ reliably between StandardTaskErrors and EnforcedTaskErrors,  $p > 0.5$ , cohen's  $d = 0.06$ , small effect size.

The modest difference (cohen's  $d = 0.67$ , medium effect size) in implicit aftereffects between the StandardTaskError and NoTaskError groups might have been due to a ceiling effect resulting from the large number of adaptation cycles (60 cycles, i.e., 480 trials) that may have obscured effects of the task error manipulations. Alternatively, the difference in implicit aftereffects between the StandardTaskError and the NoTaskError groups might only emerge after the large number of

adaptation cycles. We next conducted a follow-up experiment with a different group of naïve participants who encountered half the number of adaptation cycles (30 cycles, 240 trials) before the no-feedback block.

To evaluate the effect of the amount of training (i.e., the number of adaptation cycles) and the task error manipulations on implicit aftereffects, we ran a Training (30 adaptation cycles, 60 adaptation cycles) x Task Error (Standard, Enforced, NoTaskError) ANOVA on reaches in the first no-feedback cycle. There was a significant effect of training on the implicit aftereffect  $F_{1,136}=10.94$ ,  $p = .001$ , partial eta-squared = .074, as 60 adaptation cycles resulted in larger implicit aftereffects ( $20.6 \pm 0.6^\circ$ ) than 30 adaptation cycles ( $17.6 \pm 0.6^\circ$ ,  $p = 0.001$ , cohen's  $d = 0.55$ ), indicating that implicit learning was incomplete after 30 adaptation cycles. There was a significant main effect of Task Error,  $F_{2,136} = 7.907$ ,  $p = .001$ , partial eta-squared = .104. The implicit aftereffect was smaller with NoTaskErrors,  $16.7 \pm 0.8^\circ$ , than StandardTaskErrors,  $19.7 \pm 0.8^\circ$ ,  $p = 5.157e^{-4}$ , cohen's  $d = 0.761$ , medium-large effect size). Implicit aftereffects were also reduced with NoTaskErrors,  $16.7 \pm 0.8^\circ$ , compared to EnforcedTaskErrors,  $21.0 \pm 0.8^\circ$ ,  $p = 0.021$ , cohen's  $d = .602$ , medium effect size. Task Error did not interact significantly with Training ( $p = .74$ ).

## Discussion

Sensorimotor perturbations typically evoke task errors and sensory prediction errors at the same time, making it difficult to disentangle the effects of these distinct error sources on adaptation. In this experiment, we dissociated the effects of task errors from sensory prediction errors during target-reaching by either (1) removing task errors by moving the target to align with the cursor direction mid-movement such that the cursor always hits the target, or (2) enforcing task errors by moving the target away from the cursor mid-movement such that the cursor never hits the target, or (3) allowing standard task errors, where the target did not move during the trial. Participants adapted to a  $30^\circ$  rotation of cursor feedback across all conditions. Both removing task errors and enforcing constant task errors reduced the extent of adaptation compared to standard task errors, but this reduction was largest when task errors were removed. After adaptation, we informed participants that the perturbation had been removed: persistently adapted movements despite this knowledge suggest that an implicit change in the mapping between the motor command and the predicted sensory outcomes of the motor command has occurred. Removing task errors reduced implicit aftereffects, whilst constant task errors resulted in similar implicit aftereffects as standard task errors. We interpret this to suggest that during target reaching, the rewarding experience of task success (hitting targets), or the punishing experience of task failure (missing targets), makes a crucial contribution to implicit adaptation to sensory prediction errors.

### Removing task errors slowed adaptation

We found a dramatic reduction in the rate of adaptation to the perturbation when task errors were removed: the amount of adaptation was approximately half ( $12.5 \pm 1.2^\circ$ ) of that observed in standard conditions ( $24.2 \pm 0.8^\circ$ ). Previous studies also examined the effects of reducing task errors on adaptation, however, this was accomplished by reducing target precision, for example by having participants aim to an arc-sized target compared to a ray-sized target (Schaefer *et al.*, 2012), or a large target compared to a small target (Reichenthal *et al.*, 2016; Kim *et al.*, 2018), or by asking participants to aim where they pleased in the absence of a target (Welch, 1969). Manipulating target errors by altering target precision is known to alter spatial characteristics of movements (Fitts, 1954; Soechting, 1984), possibly due to greater uncertainty about where to aim, and reduced precision of the movement plan (Reichenthal *et al.*, 2016). Nonetheless, despite the differences in methodology, our results are consistent with previous findings: adaptation was slower when target errors were



reduced, and reaches were less adapted when the perturbation was removed. Target errors in target-reaching sensorimotor adaptation tasks therefore drive the rate and extent of compensation to sensorimotor perturbations.

### **Target errors as an intrinsic reward that contributes to implicit aftereffects**

Participants who did not experience target misses during adaptation in the NoTaskError condition showed not only reduced extent of adaptation, but also reduced amount of post-adaptation implicit aftereffects. Hence, removing the negative reward prediction errors associated with target-misses caused by a perturbation reduces implicit adaptation to that perturbation. In a similar vein, previous work has demonstrated potent effects of reward on sensorimotor remapping in owls who were either fed dead mice, or hunted live mice during a 10 week exposure to prism glasses. Despite similar feeding durations of 1 hour per day, and similar feeding behaviours (orientation towards the mice, flying, and striking the target), owls who hunted live mice showed a five-fold increase in the shift of auditory space maps in the optic tectum than owls who were fed dead mice (Bergan *et al.*, 2005). We speculate that hunting live mice in the presence of the visual perturbation ensured that the owls had to actively correct for the perturbation in order to attain the food reward. In contrast, similar to our NoTaskError group who showed smaller aftereffects than the StandardTaskError group, the owls who were fed dead mice regardless of their actions showed less remapping. In this target-hitting task, failures to hit the target are, by definition, task errors (failures to achieve the instructed task goal), and we assumed that these task errors result in a loss of intrinsic rewards associated with succeeding at the task. However, although we did not quantify to what extent are target hits intrinsically rewarding, we suspect that there is something intrinsically rewarding in hitting targets during target-reaching in typical adaptation tasks. A second issue is that we do not know if perturbations during sensorimotor adaptation evoke negative reward prediction errors (e.g., unexpected omission of the reward of hitting targets), or positive punishment errors (e.g., unexpected punishment of missing targets), or both (Galea *et al.*, 2015). Indeed, it remains unclear if there is a separate neural mechanisms for learning from punishments and learning from rewards (Palminteri & Pessiglione, 2017). Nonetheless, we believe that our results suggest that some reward and/or punishment-based process makes an important contribution to implicit adaptation to sensory prediction errors (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015). We think that this demonstrates an interaction between the system that learns from sensory prediction errors, and the system that learns from reward prediction errors. In contrast, previous theories of adaptation have considered error-based learning and reward-based learning to operate independently from each other, because while sensory prediction errors alters the mapping between motor commands and the predicted sensory consequences of the motor command, reward prediction errors alone do not (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015). This idea is supported by a large body of work showing that distinct neural systems subserve error-based learning and reward-based learning. Error-based learning is subserved by the cerebellum, as it is required for implicit adaptation of input-output maps between motor commands and sensory outcomes in response to sensory prediction errors (Martin *et al.*, 1996; Werner *et al.*, 2009; Schlerf *et al.*, 2013; Therrien *et al.*, 2015; Butcher *et al.*, 2017). Reward-based learning is thought to be subserved by the basal ganglia, which seems likely to be responsible for an action-selection policy that reduces task error (Shadmehr & Krakauer, 2008; Taylor & Ivry, 2014). The finding that the presence or absence of intrinsic rewards associated with hitting or missing targets affects implicit adaptation to sensory prediction errors suggests an alternative hypothesis: that error-based learning subserved by the cerebellum is also sensitive to reward/punishment signals from the basal ganglia. This seems plausible given the presence of disynaptic projections between the cerebellum and the basal ganglia (Bostan *et al.*, 2010; Bostan & Strick, 2010), which might allow reward signals processed by the basal ganglia to modulate implicit adaptation driven by sensory prediction errors in the cerebellum. New evidence also shows that the

cerebellum is sensitive to rewards. For example, cerebellar granule cells encode reward expectation, as their activity peaks in the pre-reward period (Wagner *et al.*, 2017). The post-synaptic targets of cerebellar granule cells are Purkinje cells, which are known to play a crucial role in sensorimotor adaptation (Herzfeld *et al.*, 2015).

Neuropsychological evidence in humans supports the possibility that the process of updating sensorimotor maps could be sensitive to reward. For example, when the neurotransmitter required for processing reward, dopamine, is deficient in Parkinson's disease, post-adaptation aftereffects are also reduced (Stern *et al.*, 1988; Contreras-Vidal & Buch, 2003; Fernandez-Ruiz *et al.*, 2003; Gutierrez-Garralda *et al.*, 2013; Roemmich *et al.*, 2014), although see (Semrau, 2011; Leow *et al.*, 2012; Leow *et al.*, 2013). Withdrawing dopamine medication in Parkinson's disease patients further reduces the size of the aftereffect (Roemmich *et al.*, 2014), demonstrating a role for dopamine reward signals in aftereffects. On the other hand, if reward prediction errors typically modulate processing of sensory prediction errors by the cerebellum, then impaired cerebellar function might not only impair the capacity for implicit adaptation to sensory prediction errors, but might also impair the capacity to respond appropriately to reward prediction errors. This is reflected in the apparent deficit in cerebellar degeneration patients in independently developing a strategy and re-aiming in response to reward prediction errors (Therrien *et al.*, 2015; Butcher *et al.*, 2017), despite intact ability to implement a strategy provided by the experimenter (Taylor *et al.*, 2010).

### Enforced task errors slowed error compensation

We enforced task errors by moving the target away from the cursor randomly clockwise or counterclockwise by 20° to 30°, such that participants could never hit the target regardless of how they moved. This manipulation also dramatically slowed error compensation, as reaches were significantly less adapted (14.3+/-0.9°) compared to standard task error conditions (24.2+/-0.8°) in the first 30 cycles of adaptation. This manipulation is similar to previous work which clamps cursor feedback to a constant offset away from the target, regardless of how participants moved (Kim *et al.*, 2017a; Morehead *et al.*, 2017), although those studies actually intended to remove task error by instructing participants to ignore the clamped cursor feedback. If participants succeed at obeying instructions to ignore the feedback, they technically do not commit any task errors (Welch, 1969). We suggest however that clamped cursor feedback actually enforces constant target errors, because participants observe their cursor constantly failing to hit the target, regardless of where they reach. These studies showed slower adaptation with clamped cursor feedback than with standard cursor feedback, but implicit adaptation did not differ with standard or clamped cursor feedback (Kim *et al.*, 2017a; Morehead *et al.*, 2017). Similarly, adaptation was slower with our enforced task error group than our standard task error group, and implicit adaptation did not differ between standard or enforced task error conditions.

### Removing task errors versus enforcing task errors

A strength of the current work is that we compared how removing task errors and enforcing task errors affected adaptation. **We suggest that** removing task errors removes the motivation for strategy use, whereas enforcing task errors deters strategy use by ensuring that all strategies are futile. **At first glance**, both methods **should be reasonably** successful in suppressing strategy use. Participants in both conditions showed no change in behaviour before and after explicit knowledge of perturbation removal. **However, several participants from the enforced task error condition reported that they did initially attempt to re-aim, but later gave up after they realized that they were missing the target regardless of what they did: this behaviour was reflected in the larger variability in the EnforcedTaskError groups (see Figure 1). Thus, the absence of a difference**

between adaptation extent and the no-feedback phase is insufficient evidence to claim that participants never attempted to re-aim during adaptation. Reaches that remain adapted despite explicit knowledge of perturbation removal thus remains a more valid measure of implicit learning than adaptation extent. We found smaller implicit aftereffects with NoTaskErrors,  $16.7 \pm 0.8^\circ$ , than with EnforcedTaskError,  $21.0 \pm 0.8^\circ$ , although the size of the effect is moderate ( $d=0.602$ ). The reason underlying this difference is unknown, but we speculate that even when task errors cannot provide a strategy for task success, task errors remain an important component to process(es) that result in implicit aftereffects. Although the current findings suggest that target hits/misses modulate implicit adaptation to sensory prediction errors, we do not yet know if implicit adaptation is driven by a single process that is sensitive to target hits/misses, or if implicit adaptation is driven by multiple processes which are differentially sensitive to target hits/misses: this possibility awaits future study.

### **Intrinsic versus extrinsic rewards and punishments**

We operationalized target hits as intrinsically rewarding and target misses to be intrinsically punishing, without providing any additional extrinsic rewards or punishments such as monetary gains or monetary losses. We do not know if and how extrinsic rewards or punishments might interact with intrinsic rewards or punishments during learning. The majority of previous work examining the role of reward on motor learning manipulated extrinsic rewards and punishments without manipulating intrinsic rewards and punishments (e.g., Wachter *et al.*, 2009; Abe *et al.*, 2011; Galea *et al.*, 2015; Nikooyan & Ahmed, 2015; Gajda *et al.*, 2016; Steel *et al.*, 2016; Song & Smiley-Oyen, 2017). One possibility is that extrinsic rewards and punishments affect learning via additive or subtractive effects on intrinsic reward processes. This is because extrinsic rewards and punishments only affected learning when they were meted out in conjunction with task errors: providing rewards or punishments that were not contingent upon task errors did not alter learning (Galea *et al.*, 2015; Nikooyan & Ahmed, 2015). Alternatively, extrinsic and intrinsic rewards might exert independent effects on learning. These possibilities await future study.

### **Manipulating target error to dissociate explicit from implicit learning**

Here, we removed the contingency between task error and participant behaviour: removing the contingency between task error and participant behaviour appears reasonably effective in suppressing the tendency to explicitly re-aim. We think that the current method of manipulating target errors is a valuable adjunct to previously established methods of separating the effects of explicit re-aiming from implicit adaptation in visuomotor rotation experiments. Previous methods of isolating implicit adaptation have some limitations. For example, self-reporting aiming directions (Taylor *et al.*, 2014) might alert participants to the possible benefits of re-aiming. Clamping cursor feedback (Morehead *et al.*, 2017) requires participants to fully understand instructions that the direction of the cursor is invariant regardless of their movements. Reducing movement preparation time (Fernandez-Ruiz *et al.*, 2011; Haith *et al.*, 2015; Huberdeau *et al.*, 2017; Leow *et al.*, 2017) may not suppress explicit learning with a narrow distribution of targets (Leow *et al.*, 2017). Future studies should test the limitations of the current method. **For example, the enforced task error manipulation does not preclude participants from trying to re-aim: indeed, several participants from the enforced task error condition reported attempting to re-aim, but giving up when realizing that they were missing the target regardless of what they did. Furthermore, disincentivising strategy use by ensuring target hits may not prevent volitional re-aiming if participants were intent on doing so, although self-reports for the NoTaskError participants suggests that they did not try to re-aim.**

## Limitations

There are some limitations in this study that warrant attention. First, across all groups, we provided online cursor feedback only after participants moved at least 4cm of the 9cm start-target distance, because piloting with the EnforcedTaskError condition showed that some individuals slowed their movements to make online corrections to hit the target, thus invalidating the EnforcedTaskError manipulation. The absence of cursor feedback in the first 4cm of movement might have limited the amount of implicit adaptation, as many studies have shown that cursor feedback upon movement completion (i.e., endpoint cursor feedback) results in less implicit adaptation than continuous, full cursor feedback (e.g., Hinder *et al.*, 2008; Hinder *et al.*, 2010; Peled & Karniel, 2012; Schween *et al.*, 2014). Second, we employed a large cursor that was the same size as the target, reducing the resolution of the cursor position. Third, we only tested one small 30° cursor perturbation: previous work comparing implicit adaptation with cursor perturbations of different sizes have shown similar amounts of implicit adaptation with cursor perturbations of different sizes (e.g., Bond & Taylor, 2015; Morehead *et al.*, 2017), although the amount of implicit adaptation does appear to scale with the size of the cursor perturbations when it is less than 6°(Kim *et al.*, 2017a). More work is needed to see if the findings shown here replicate under conditions of full online cursor feedback provided by a small cursor, as well as with cursor perturbations of different sizes.

## Summary

In summary, we showed that the intrinsic reward of hitting or missing targets during target-reaching in sensorimotor adaptation affects implicit aftereffects resulting from exposure to sensory prediction errors. Hence, even though reward prediction errors alone are not sufficient to result in sensory remapping (Izawa & Shadmehr, 2011), **rewards might** contribute to changes in implicit aftereffects, possibly by increasing sensitivity to sensory prediction errors.

Conflict of interest statement: The authors report no conflict of interest.

Abbreviations list: StandardTE (Standard Task Errors), NoTE (No Task Errors), EnforcedTE (Enforced Task Errors).

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**Data statement:** Data is available, and uploaded online on the EJM online system.

### Author contributions:

Study conception and design: Leow, Carroll. Acquisition of data: Leow.

Analysis and interpretation of data: Leow, Marinovic, de Rugy, Carroll. Drafting of manuscript: Leow.

Critical revision: Leow, Marinovic, de Rugy, Carroll

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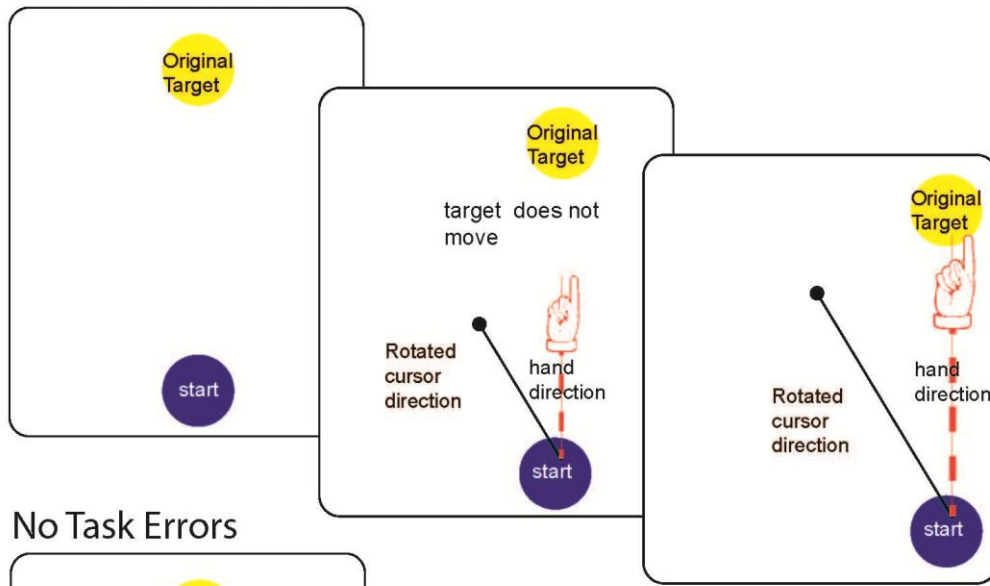
Widmer, M., Ziegler, N., Held, J., Luft, A. & Lutz, K. (2016) *Rewarding feedback promotes motor skill consolidation via striatal activity*. Elsevier B.V.

### Figure Legends

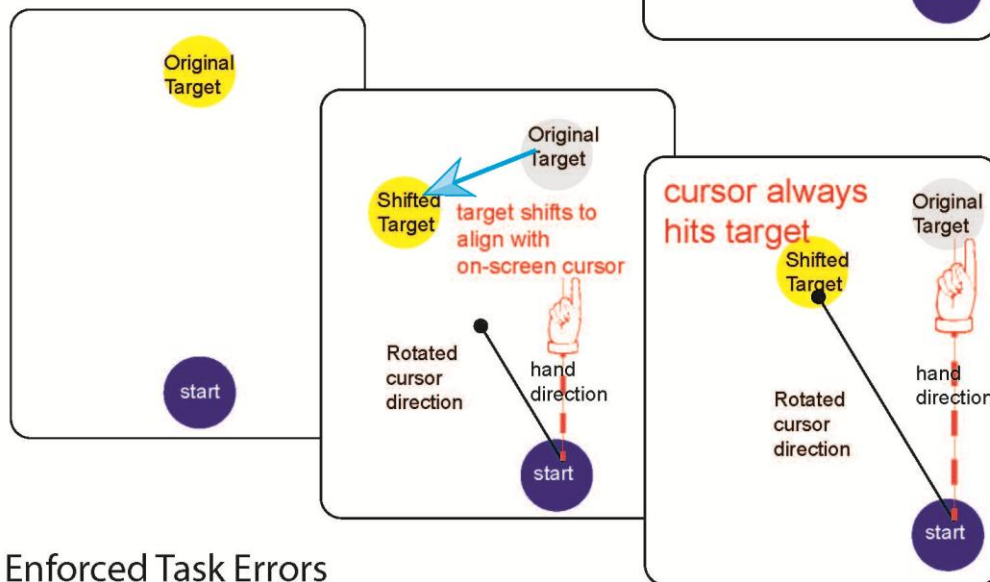
Figure 1. Experimental conditions. StandardTaskError (top panel): target remained stationary within a trial. NoTaskErrors (middle panel): target shifted mid-movement (i.e., when the cursor had moved 4cm out of the 9cm start to target distance) to align with on-screen cursor direction, such that the cursor always hit the target. EnforcedTaskErrors (bottom panel): target shifted mid-movement away from on-screen cursor direction, randomly by 20 to 30° (clockwise in approximately 50% of the trials, and counterclockwise in approximately 50% of trials), such that the cursor could not hit the target.

Figure 2a. Group mean $\pm$ SEM for reach directions across all cycles (1 cycle=8 trials=1 visit to each of the 8 targets). Reaches closer to 30° represent more complete error reduction. Adaptation was least complete with NoTaskErrors (red), followed by EnforcedTaskErrors (blue) and StandardTaskErrors (green). 2b. Asymptote (mean reach direction in the last 5 adaptation cycles). 2c. Implicit aftereffects (mean reach direction in the first no-feedback cycle). Implicit aftereffects in the NoTaskError group was reduced compared to the StandardTaskError group and the EnforcedTaskError group. 2d. Volitional disengagement of explicit learning, as quantified by the change in reach direction upon notification that the cursor rotation had been removed. 2e. Group mean $\pm$ SEM for reach directions across all cycles for the follow-up experiment with 30 instead of 60 adaptation cycles. 2f. Adaptation extent, quantified in the last 5 of the 30 adaptation cycles. 2g. Less implicit aftereffects was evident with NoTaskErrors than with StandardTaskErrors. 2h. The NoTaskError group also did not show volitional disengagement of explicit learning. Error bars were standard errors of the mean for cycle by cycle data in 2a and 2e. Error bars were 95% confidence intervals for 2b-d and 2f-h.

### Standard Task Errors



### No Task Errors



### Enforced Task Errors

