Title: Task errors drive memories that improve sensorimotor adaptation.

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Abstract.

Traditional views on how humans adapt movements to perturbations of sensory feedback emphasize a fundamental role for automatic, implicit correction of sensory prediction errors. However, it is now clear that adaptive behaviour also involves deliberate, strategic movement corrections. Such strategic processes have recently been argued to underlie the latent retention of sensorimotor adaptation, evident in improved adaptation to previously encountered perturbations; a phenomenon termed “savings”. It remains unclear, however, whether savings results from prior experience of sensory prediction errors, task errors, or both. Here, we used perturbations of target locations and hand position feedback during reaching to dissociate the contributions of task and sensory prediction errors to latent sensorimotor memory. We show that prior learning to correct for task errors is required to improve adaptation to rotated hand position feedback, whereas a history of sensory prediction errors is neither sufficient nor obligatory for savings. A history of correcting for task errors, induced by experimentally perturbing the target location instead of perturbing sensory feedback of movement, improved adaptation to visuomotor perturbations that were never before encountered. Limiting movement preparation time further showed that this learning consists of two distinct components: 1) a strategic component that is flexible enough to facilitate corrective responses in the opposite direction, but that requires substantial preparation time, and 2) a set of inflexible, cached, stimulus-response associations between targets and reach directions, that can be expressed under time-pressure when similar task conditions are experienced. The results emphasise that adaptive responses to sensorimotor perturbations take multiple forms.

Introduction

A large body of knowledge created in the last 25 years about motor learning

has been drawn from the paradigm of sensorimotor adaptation. Here, a systematic perturbation is applied to the visual representation of movement (von Helmholtz & Southall, 1924; Cunningham, 1989), or to limb dynamics (Dietz *et al.*, 1994; Shadmehr & Mussa-Ivaldi, 1994), such that the sensory consequences of motor commands are changed. This necessitates adaptive motor responses in order to restore effective movement under the new conditions. Given changes in the environment and the body, such adaptive processes are essential to sustain successful movement in the natural world. There are, however, long standing questions over the extent to which principles of sensorimotor adaptation apply to other forms of motor learning; especially to the acquisition of novel motor skills. This issue is important because novel skill acquisition is of considerable practical relevance: during rehabilitation (Krakauer & Carmichael, 2017), sport (e.g., learning to serve a tennis ball), and industry (e.g., learning to control a back-hoe).

A key piece of evidence pertinent to the question of how sensorimotor adaptation relates to other forms of motor learning is the extent to which exposure to sensorimotor perturbations generates long-lasting memories. Sensorimotor memory is often operationalised as improved adaptation when re-encountering a similar perturbation, and the phenomenon, commonly termed savings, is well documented (Flook & McGonigle, 1977; Brashers-Krug *et al.*, 1996; Kojima *et al.*, 2004; Mawase *et al.*, 2014; Roemmich & Bastian, 2015; Seidler *et al.*, 2016; Cassady *et al.*, 2018; Day *et al.*, 2018). Importantly, the sensorimotor memories implied by savings are latent, because the benefit of previous exposure persists even after behaviour is returned to the naïve state by removing the perturbation for many trials (Zarahn *et al.*, 2008), even a year after the initial encounter (Landi *et al.*, 2011; Maeda *et al.*, 2018). A latent form of memory for sensorimotor perturbations is both obligatory for success given non-stationarity of our environment, and reminiscent of new motor skill memories, which can be flexibly expressed according to context.

Although a long history of work has sought to identify the mechanisms that underlie savings (e.g., Smith *et al.*, 2006; Huang *et al.*, 2011; Hadjiosif & Smith, 2013; Herzfeld *et al.*, 2014; Mawase *et al.*, 2014; Huberdeau *et al.*, 2015a; Orban de Xivry & Lefevre, 2015), the topic remains controversial. One influential proposal was the idea that savings occurs because specific actions are associated with task success during initial adaptation to the perturbation, and that these actions are recalled upon task failure when a related perturbation is subsequently encountered

(Huang *et al.*, 2011). An alternative idea is that exposure to a new sensorimotor environment induces a form of “meta-learning”, in which the structure of the perturbation is encoded in memory to assist subsequent adaptation. More recently, savings has been attributed to changes in the sensitivity to errors (Gonzalez Castro *et al.*, 2014; Herzfeld *et al.*, 2014). According to this idea, experiencing a systematic sequence of errors generates a memory of errors, which increases sensitivity to those errors and the gain of error correction when reencountering similar errors (Gonzalez Castro *et al.*, 2014; Herzfeld *et al.*, 2014).

Despite the importance of the phenomenon of savings for the broad field of motor learning, interest in the processes that underlie the effect has declined since Morehead et al (2015) and Haith et al (2015) provided compelling evidence that savings in standard visuomotor rotation conditions is dominated by volitional, strategic selection of actions that can restore task success. For example, leftward displacement of visual feedback causes a person to miss the target to the left, they tend to deliberately aim to the right of the target to counteract the error (Uhlarik, 1973). Using cues to signal perturbation onset prompted rapid re-selection of the adapted movement on the first trial, even before participants re-experienced the previously encountered error (Morehead *et al.*, 2015). Similarly, suppressing strategy use by limiting movement preparation time prevented the expression of savings (Haith *et al.*, 2015). If savings were solely a manifestation of deliberate strategy use, then “cognitive” functions which determine how successfully one might acquire and implement strategies would be central to acquisition of latent sensorimotor memories: non-strategic “motor” processes would thus be of less importance.

But is the conscious awareness of a strategy, to apply a corrective movement that already exists within the participant’s motor repertoire, really all that is retained when a person adapts movement to a perturbation? Or are there components of savings that are less amenable to conscious control? Savings is evident in alternative sensorimotor adaptation contexts where the required corrective movement is less obvious, such as force field and split-belt treadmill paradigms (Mawase *et al.*, 2014; Roemmich & Bastian, 2015; Cassady *et al.*, 2018; Day *et al.*, 2018) or in saccadic adaptation (Kojima *et al.*, 2004). This suggests the existence of a component to long-term retention of latent sensorimotor memories that is less accessible to conscious awareness. If there are indeed multiple components to long-term sensorimotor memories, then what are the necessary conditions for their

encoding and expression? A systematic approach to address this question requires experiments to dissociate the contributions of the different types of errors that drive sensorimotor adaptation, both during the initial exposure to the perturbation and when the putative latent learning is subsequently expressed. Sensorimotor perturbations, by definition, evoke sensory prediction errors (i.e., discrepancies between predicted sensory outcomes of movements and actual sensory outcomes of movements), but can also lead to task performance errors (i.e., a failure to successfully accomplish a task). Which of these errors are required for the encoding and re-expression of long-term sensorimotor memories?

Here, we show that experience of task errors during an initial exposure to visuomotor rotation is necessary for latent retention of visuomotor memory, and that it is not necessary to reexperience task errors in order to subsequently express this learning. Further, we show that a history of correcting for task errors, provoked by perturbing target location rather than sensory feedback of movement, can evoke faster adpatation to a subsequent sensorimotor perturbation, even when participants have no prior experience of this sensorimotor perturbation. This learning appeared at first glance to show hallmarks of a volitionally controlled strategy: it was flexible enough to accommodate a different reach solution at training and at test. However, this flexibility disappeared when we limited movement preparation time: performance was worse than naïve as participants continued to re-engage the now-maladaptive reach solution that they had learned previously to associate with restoration of success in the task. Thus, improved adaptation to sensorimotor perturbation requires a history of compensating for task errors, and the latent sensorimotor memories that underlie improved adaptation to subsequent perturbations can take at least two distinct forms, 1) volitionally controlled, flexible strategies and 2) inflexible stimulus-response associations that are less amenable to volitional control.

Methods and Materials

Participants

There were a total of 132 participants (75 female, age range 17-34 years, mean age 20.6). 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 a 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 targets, the start circle, and hand cursor 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 reduce possible effects of fatigue.

General Trial Structure

While grasping the robot arm, participants moved their hand-cursor (0.5cm radius red circle) from the central start circle (0.5cm radius white circle) to the targets (0.5cm radius yellow circles). Targets appeared in random order at one of eight locations (0°, 45°…. 315°) at a radius of 9 cm from a central start circle. At the start of each trial, the central start circle was displayed. If participants failed to move their hand-cursor to within 1cm of the start circle after 1 second, the robotic manipulandum 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. Across all experiments, we used a classical timed-response paradigm (e.g., e.g., Schouten & Bekker, 1967) to manipulate movement preparation time during the planar reaching task (Favilla & De Cecco, 1996). 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 monitor display latency (27.6 ± 1.8ms), 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.*, 2017). No visual feedback about movements was available when trials were aborted, and so such trials were repeated at the end of the cycle. We enforced long movement preparation times across most conditions to prevent the possibility that the task error manipulation resulted in self-selection of different movement preparation times. Under these conditions, participants had ample opportunity (i.e. time for movement preparation) to use explicit strategies.

Across all conditions, cursor feedback was displayed after the hand had moved 4cm from the start to target (located 9cm away from the start). At this point, the direction of cursor velocity was measured to define target movements in some conditions as described below. During **StandardTaskError** conditions, the target remained stationary throughout the trial, such that whether or not participants hit the target was contingent on the participant’s reach direction. During **NoTaskError** conditions, the target was shifted to align with the direction of cursor velocity, measured at 4cm into the movement. 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. During **EnforcedTaskError** conditions, the target was shifted randomly by 20°–30° (counterclockwise in half of the trials, clockwise in half of the trials) relative to the cursor direction when the hand had moved 4 cm from the start. 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. In Experiments 3 and 4, we imposed systematic task errors without any perturbation of the hand-cursor relationship: the target was moved during the movement by 30° relative to the original target position, always in the same direction (clockwise for half of all participants, counterclockwise of half of all

participants, counterbalanced): no rotation of the visual feedback of movement was imposed when this occurred.

To familiarize participants with the equipment and the timed-response paradigm, all participants were first allowed a familiarization block comprising a maximum of 6 cycles. One cycle consisted of 1 trial to each of the 8 targets, and target order was random within each cycle. Participants were explicitly instructed to make shooting movements so that the cursor passed 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. After familiarisation, 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. **Baseline** (6 cycles): no rotation of visual feedback. **Training** (60 cycles): For experiments 1 & 2, 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. For experiments 3-4, no cursor rotation was applied during this training phase, but a 30° rotation of target position relative to the original target position was applied mid-movement. Half of all participants encountered a clockwise 30° rotation and half encountered a 30° counterclockwise rotation. **No feedback** (6 cycles): Upon leaving the start circle, no feedback about movements was 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 as soon as it leaves the start circle, so please move straight to the target”. **Washout**: Cursor position feedback was restored, but the 30° rotation of cursor was removed. For Experiments 1 and 2, to prevent the experience of washout-related task errors, task errors were removed across all conditions (i.e., the target position shifted mid-movement to ensure that the cursor always hit the target). The length of the washout block was the same as the adaptation block (60 cycles). For Experiments 3 and 4, participants had no prior experience of the cursor rotation, only task errors, and they could volitionally reach straight to the target by the end of the no-feedback block, thus it was unnecessary to employ a long washout with the no-task-error manipulation to avoid exposure to errors related to abrupt removal of the

perturbation: we thus provided 12 washout cycles without mid-movement target shifts. **Test** (60 cycles): the 30° rotation of cursor feedback was imposed (half of all participants encountered a clockwise 30° rotation and half encountered a 30° counterclockwise rotation). Between each block, there was a small delay to allow for experimental instructions and loading of the computer code for different experimental blocks.

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. 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. Experiment1: StandardTaskErrors: 0.62%, NoTaskErrors 0.11%, EnforcedTaskErrors: 1.73%; Experiment2: TrainStandardTaskErrors: 0.29%, TrainEnforcedTaskErrors: 0.62%; TrainNoTaskErrors: 0.17%; Experiment 3: Same: 0.30%, Different: 0.20%. Experiment 4:ShortDifferent: 3.82%; ShortSame: 4.31%, ShortNaive:4.59%). 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 conversion to percent adaptation (see below). For graphing purposes, reach directions for participants who experienced counterclockwise rotations (30°) were sign-transformed and pooled with data for participants who experienced counterclockwise (30°) rotations: values closer to 30° indicate more complete adaptation.

For all blocks except the test block, we estimated adaptation performance as percent adaptation, which quantifies reach directions relative to the ideal reach direction (as shown inHadjiosif & Smith, 2013).

$$naive\ percent\ adaptation = 100\% \times \frac{reach\ direction - baseline\ bias}{ideal\ reach\ direction - baseline\ bias}\ .$$

For the test block, we were interested in savings, which is improved learning at test compared to naïve. Even with exposure to the same number of no-rotation trials at washout as at training (480 trials), washout was often incomplete. Incomplete washout can inadvertently magnify estimates of savings. Estimates of savings thus needs to take into account the extent of washout (Haith *et al.*, 2015).

We estimated percent adaptation for the test block as follows, where reach biases in the washout phase were estimated as the mean of the final 3 cycles of the washout block.

$$test\ percent\ adaptation = 100\% \times \frac{reach\ direction - washout\ bias}{ideal\ reach\ direction - washout\ bias}$$

To evaluate savings (improved learning at test compared to naïve), we ran ANOVAs on all adaptation cycles, with factors block (Naïve, Test) x Phase (Early, Middle, Late) x Cycle (Cycle 1…20) ANOVAs, with greenhouse-geisser corrections applied where appropriate. Where there was a significant main effect of block, post-hoc t-tests were run on the mean of the first 5 cycles of the naive/adaptation block, as savings tends to be most evident at initial exposure/re-exposure to the rotation in visuomotor rotation paradigms (Krakauer *et al.*, 2005; Huberdeau *et al.*, 2015a). For Experiment 1, test block adaptation was compared to naïve block adaptation within the same group of participants. For Experiment 2, test block adaptation with a certain task error manipulation was compared to naïve adaptation from a different group with equivalent task error manipulations. Specifically, the TrainStandardTE group and the TrainEnforcedTE group experienced no task errors at test, and thus were compared to the naïve no task error block from the TrainNoTaskErrors group. The TrainNoTaskErrors group experienced standard task errors at test and thus were compared to the naïve standard task error block in the TrainStandardTaskErrors group. Similarly, for Experiment 3, test block adaptation with standard task errors was compared with the naïve standard task error block in the TrainStandardTaskError group from Experiment 2. For Experiment 4, test block adaptation with short preparation time and standard task errors were compared with data from a separate control group who experienced the same short preparation time and standard task error conditions, but who were naïve to any training to reduce task errors or sensory prediction errors.

A common alternative measure of savings is to assess for increases in rate constants, obtained by fitting the data to exponential functions. Rate constant analyses were not used here for the following reasons. For datasets where savings is evident as immediate adaptation in the first cycle upon perturbation exposure (Landi *et al.*, 2011; Huberdeau *et al.*, 2015a), rate constants are typically small because the rapid initial adaptation is not captured by the fit. This can give the

erroneous impression that savings is absent, and this situation was apparent in some of our data. When we tried to avoid this problem by fixing the fit parameter that reflects the y value when x = 0 as the mean reach direction in the immediately previous no-rotation cycle, the fits poorly characterized the data. Furthermore

Statistical analyses were performed with SPSS. Graphs were plotted with GraphPad Prism version 7.00 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com.

Results

Experiment 1: Task errors are important for savings

In Experiment 1, we asked whether savings would be present if adaptation was learnt in the absence of task errors, or with task errors that were enforced regardless of the participants' actions. During training, all participants were exposed to a 30° rotation of cursor feedback. In the StandardTaskError condition, since the target was not moved within a trial, task errors were allowed to vary contingent upon participants' responses to the cursor perturbation (Figure 1B). Task errors were enforced in the EnforcedTaskError condition by moving the target mid-movement so that the cursor always missed the target by 20-30° (Figure 1E). Task errors were removed in the NoTaskError condition by moving the target to align with the cursor trajectory mid-movement (Figure 1H). After initial exposure to the visuomotor rotation, behaviour was returned to the unadapted state by removing the cursor rotation in a washout phase. During this washout, we also employed the NoTaskError manipulation across all groups to prevent experience of task errors upon abrupt removal of the cursor rotation. At the test block (i.e., the second exposure to the visuomotor rotation) we applied the same task error manipulations that each group experienced when they were initially exposed to the perturbation.

Reach directions across all cycles for groups are shown in Figure 1A. Both removing task errors and enforcing task errors slowed adaptation compared to experiencing standard task errors that were contingent upon the corrective responses of the participant. One participant from the no task error group did not move towards the presented target in the cycles 41 to 47, which resulted in the variability that is apparent in the group average plot. The analysis outcomes were similar with and without this dataset.

To evaluate savings (i.e., improved test adaptation compared to naïve), we

ran separate ANOVAs for each task error group, with the factors Block (naive, test) x Phase (early, middle, late) x Cycle (1…20), focusing on main effects of block and significant interactions with the factor block.

With standard task errors, percent adaptation at test improved compared to naive primarily in the first few cycles, similar to previous work (Krakauer *et al.*, 2005), (block x phase x cycle interaction, $F(7.6,84.2) = 2.58$, $p = 0.0158$, partial η-squared = 0.19). Post-hoc t-tests run on the mean of first 5 cycles showed a tendency to increased percent adaptation (naïve: 37.5+/- 3.9%, test: 53.4+/-8.6%, p=.0554, cohen's d= 0.618).

With enforced task errors (Figure 1H), overall adaptation at test did not differ reliably compared to naïve, as shown by no reliable main effect of block (block, $F(1,11)=2.855$, $p=0.119$, partial η-squared = 0.2) and no reliable interactions with block.

With no task errors (Figure 1I), adaptation at test was worse overall (mean of the entire test block: 46.3+/-5.1%) compared to naïve (mean of the entire naïve block, 53+/-3.6%, figure 1I), significant main effect of block, $F(1,11)=5.95$, $p=.033$, partial η-squared = 0.35. Post-hoc t-tests on the mean of the first 5 cycles showed no reliable difference in percent adaptation from naïve (17.7+/-3.1%) to test (13.1+/-2.8%), $t(11)=1.08$, $p=.303$, cohen's d =0.3.

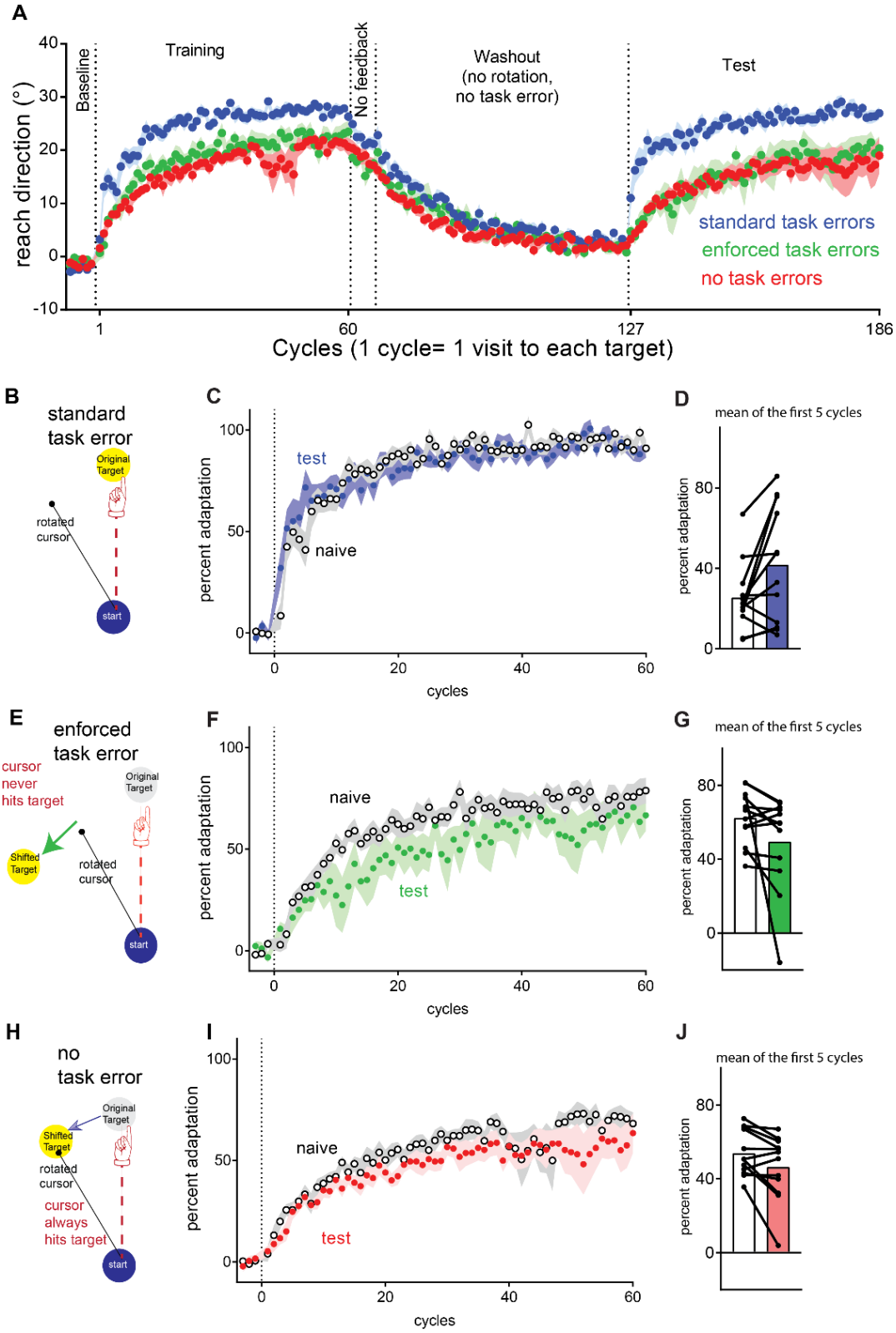

Figure 1. Experiment 1: Savings occurred with standard task errors, but not with no task errors or enforced task errors. At both training and test (i.e., during exposure to a 30° cursor rotation, participants were exposed to either standard task errors (B), enforced task errors (E), or no task errors (H). Cycle averaged reach directions across all blocks (A). Cycle averaged percent adaptation compared to naïve white circles) (C, F, I), and mean percent adaptation averaged across cycles (D, F G). Improved adaptation (greater percent adaptation) compared to naïve was evident with standard task errors (C & D), but not with enforced task errors (F&G), and not with no task errors (I & J). For D, F, G, error bars=95% CI. All other error bars are SEM.

Thus, despite exposure to the same cursor perturbation, and therefore experience of sensory prediction errors in all groups, savings was only evident in the group that experienced task errors as a consequence of sensorimotor perturbation. Task errors evoked by perturbations of sensory feedback thus appear to play an important role in savings.

Experiment 2: Task errors are required at encoding but not at retrieval.

Experiment 1 showed that during adaptation to perturbations, task errors that directly result from those perturbations play an important role in savings. A few interpretations are possible. First, task errors might act as a retrieval cue to trigger the memory that is responsible for savings (Huberdeau *et al.*, 2015a). Second, task errors might be necessary to encode a memory that is responsible for savings. Third, task errors might be necessary both at encoding and at retrieval for savings: savings can only occur when previously experienced task errors are revisited. We dissociated these possibilities in Experiment 2. Task errors were manipulated either at training or at test to identify whether savings requires prior experience of task errors during first exposure to a perturbation (when a memory is first “encoded”) or when the perturbation is re-encountered (when a memory is “retrieved”). A TrainStandardTaskError group (n=12, 6CW, 6CCW) was deprived of task errors at test (target was shifted mid-movement so that the cursor always hit the target), but were provided standard task errors at training (i.e. no target shifts): absence of savings here would suggest that task errors are necessary as a retrieval cue for savings. A TrainNoTaskError group (n=12, 6CW, 6CCW) was deprived of task errors at training, but experienced standard task errors at test (target did not move mid-movement): absence of savings here would suggest that the task errors are not required as a retrieval cue, but are a necessary component to encoding a memory that results in savings. Does savings result from the experience of task errors alone, or does savings require learning to correct for task errors? To test this, a TrainEnforcedTaskError group (n=12,6CW, 6CCW) were provided with enforced task errors at training (target always moves away from the cursor mid-trial, such that they could never succeed in reducing task errors), and were tested for savings in the absence of task errors. After training, all groups encountered 6 no-feedback cycles and 60 no-rotation washout cycles with no task error, and then re-encountered the same cursor rotation as they experienced at training. To evaluate savings, test

performance was compared to the naive adaptation of another group who experienced the same task error conditions, using separate Group x Phase (early, middle, late) x Cycle (1…20) ANOVAs. Specifically, the no task error test phase from the TrainStandardTaskError and the TrainEnforcedTaskError groups was compared to the no task error training phase of the TrainNoTaskError group. The standard task error test phase from the TrainNoTaskError group was compared to the standard task error training phase of the TrainStandardTaskError group.

Figure 2C shows that in the TrainStandardTaskError group, standard task errors at training resulted in better-than-naïve adaptation at test, even in the absence of task errors at test (significant main effect of group: $F(1,22)=10.211$, $p= .004$, partial eta-squared =.314. Post-hoc t-tests on the first 5 cycles showed better adaptation at test (36.5+/-8%) compared to naive (15.2+/-1.5%), $t(22)= 2.61$, $p= 0.016$, cohen's $d=1.065$. Thus, a history of task errors improved re-adaptation to a cursor rotation even when the perturbation did not cause any task errors upon second exposure.

In the TrainEnforcedTaskError group (Figure 2E), no savings was evident, as adaptation did not reliably improve compared to naïve, as Group (TrainEnforcedTaskError, Naïve) x Phase x Cycle ANOVA showed no significant main effect of group, $F(1,22)=1.20$, $p=.285$, partial eta-squared=.052, no significant interactions with group, all $p >.4$). Enforcing task errors at training thus did not appear to improve adaptation compared to naïve when tested without task errors. Thus, merely experiencing task errors, without learning to correct for those task errors, was not sufficient to evoke subsequent savings.

In the TrainNoTaskError group (Figure 2I), no savings was evident, as adaptation did not reliably improve compared to naïve, as Group (TrainNoTaskError, Naïve) x Phase x Cycle ANOVA (no significant main effect of group, $F(1,22) = 1.38$, $p = 0.25$, partial η-squared = 0.05, no significant interactions with group). Thus, depriving participants of task errors when they were first exposed to the cursor rotation at training resulted in no savings despite the subsequent presence of standard task errors at test.

Thus, a history of adapting movements to correct task errors appears necessary to encode learning that improves adaptation to a previously experienced

visuomotor rotation. The presence of task errors appears unnecessary to retrieve this learning.

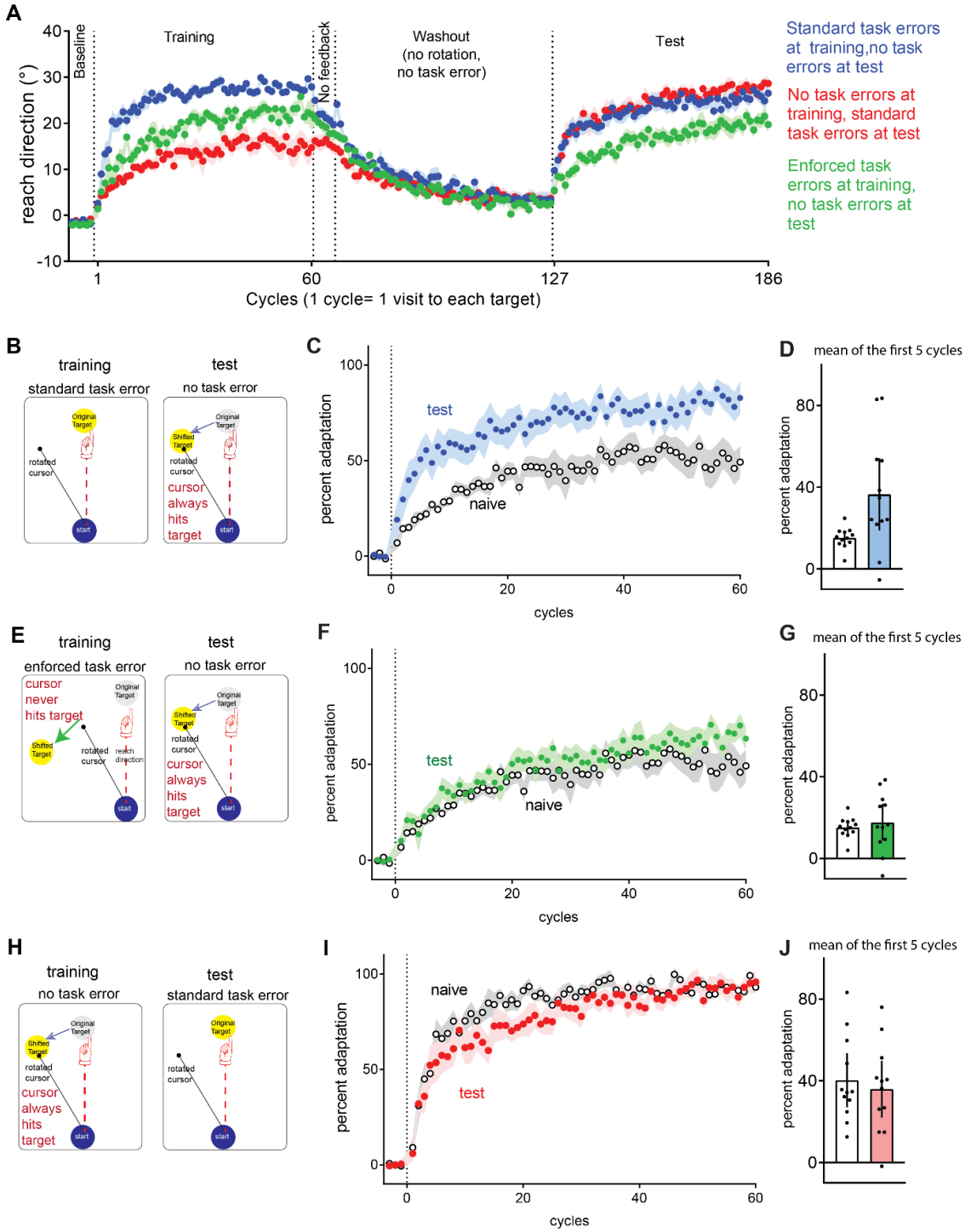

Figure 2. Experiment 2 showed that savings requires a history of adaptation to task errors. During initial exposure to the cursor rotation (training), participants experienced task errors (either standard task errors **(B)** or enforced task errors **(E)**, or experienced no task errors **(H)**. At re-exposure to the cursor rotation (test), participants who experienced task errors at training were now deprived of task errors **(B & E)** whereas participants who were deprived of task errors at training were now provided task errors. **(A)** Cycle averaged reach directions across all blocks. Note that task errors were removed at washout in all groups to ensure that abrupt removal of the perturbation would not inadvertently evoke task errors. Clear symbols and white bars indicate naïve adaptation. **(B).** Even without task errors at test, a history of standard task errors at training improved subsequent adaptation, (greater percent adaptation in C & D**).** In contrast, adaptation was not improved in the group who experienced a history of enforced task errors that could not be corrected for (F&G). Adaptation was also unimproved without a history of task errors at training, despite the presence of task errors at test. (I & J). For D, F, G, error bars=95% CI. All other error bars are SEM.

Experiment 3: Previous learning to correct for task errors can evoke savings.

Recent work suggests that savings in visuomotor rotation primarily reflects the deliberate application of a strategy, where participants explicitly re-aim to the one side of a target to counteract the rotation of cursor feedback (Haith *et al.*, 2015; Morehead *et al.*, 2015). This view considers the role of implicit adaptation to sensory prediction errors as secondary to the role of strategy in savings, and would interpret the presence/absence of savings with task errors in Experiments 1 and 2 to be because task errors provoke the formation of explicit strategies. An alternative view is that task errors alter the sensitivity to sensory prediction errors (Leow *et al.*, 2018; Kim *et al.*, 2019), and increased sensitivity to these errors produce savings (Herzfeld *et al.*, 2014). We cannot dissociate between the two alternative explanations based on data from Experiments 1 and 2 alone because task errors here were not wholly independent of sensory prediction errors; the task error manipulations were always made in the presence of a perturbation of the hand-cursor relationship (which therefore induced sensory prediction errors). Thus, we next examined how learning to correct for task errors alone, in the absence of sensory prediction errors (i.e., in the absence of any perturbation of the hand-cursor relationship), affected subsequent adaptation to a visuomotor rotation.

In Experiment 3, we did not perturb the cursor at training, but enforced systematic task errors that could be counteracted by a re-aiming strategy: the target always moved away by 30° from the original target location mid-movement: participants could correct these task errors by re-aiming 30° away from the original target (see Figure 3a). For one group of participants, the reach solution needed to hit a given target after it jumped mid-movement was the same reach solution needed to counteract the cursor rotation in the test block (**Same**, n=12, 6 CW, 6 CCW). For example, if the target jump at training was 30° counterclockwise, then the cursor rotation at test was 30° clockwise (thus requiring a counterclockwise compensatory hand movement). To test whether this learning is flexible enough to accommodate a different reach solution, we had another group of naïve participants (**Different**, n=12, 6 CCW, 6CW), where the reach direction required to hit targets at training was opposite to that at test. Pilot testing revealed substantial individual differences in how quickly participants developed a strategy to re-aim at training. Thus, if the experimenter observed that participants had yet to show successful re-aiming by trial

180 of the 480-trial training block, the experimenter explicitly instructed participants that a strategy may be needed to hit the target. This explicit instruction was required in 2 of the 12 participants in the Same group, and 6 of the 12 participants in the Different group. Here, the instruction was given without exposure to the cursor perturbation but after exposure to the *task* error. At the test block, no instructions about re-aiming were provided. To quantify savings, we compared percent adaptation at test to naïve controls who experienced similar task error manipulations (i.e., the naïve adaptation block from the group who experienced standard task errors at training in Experiment 2).

Figure 3B shows reach directions in all cycles. After instructing participants that the task error manipulation had been removed, reach directions reverted rapidly back to baseline in the no-feedback block. This illustrates that the re-aiming response can be switched off immediately upon instruction.

Despite being naïve to the cursor rotation, improved adaptation was evident when the reach solution at test was the same as training (Figure 3C), Phase x Cycles x Group interaction, $F(11.1,245.3) = 2.63$, $p = 0.00318$, partial η-squared = 0.1. Post-hoc t-tests on the mean of the first 5 cycles showed better adaptation at test (69.1+/-8.7%) than naïve (40.3+/-6%), $t(22) = 2.722$, $p=0.012$, cohen's d = 1.111). Similarly, improved adaptation was evident when the reach solution at test was opposite to that at training (Figure 3E), main effect of group, $F(1,22) = 8.11$, $p = 0.009$, partial η-squared = 0.26, Cycle x Group interaction, $F(8.4,185.9) = 2.92$, $p = 0.003$, partial η-squared = 0.11, Phase x Cycles x Group interaction, $F(11.3, 250) = 1.69$, $p = 0.073$, partial η-squared = 0.07. Post-hoc t-tests on the mean of the first 5 cycles showed better adaptation at test (72.2+/-6.7%) than naïve (40.3+/-6%), t(22)-3.56, $p=0.002$, cohen's d=1.453.

Hence, previous learning to counteract task errors was sufficient to improve subsequent adaptation to a visuomotor rotation, even when participants were naïve to perturbation-induced sensory prediction errors. This learning was flexible: it elicited savings even when the reach solution required to hit a given target at training was different from the reach solution required to hit that target at test.

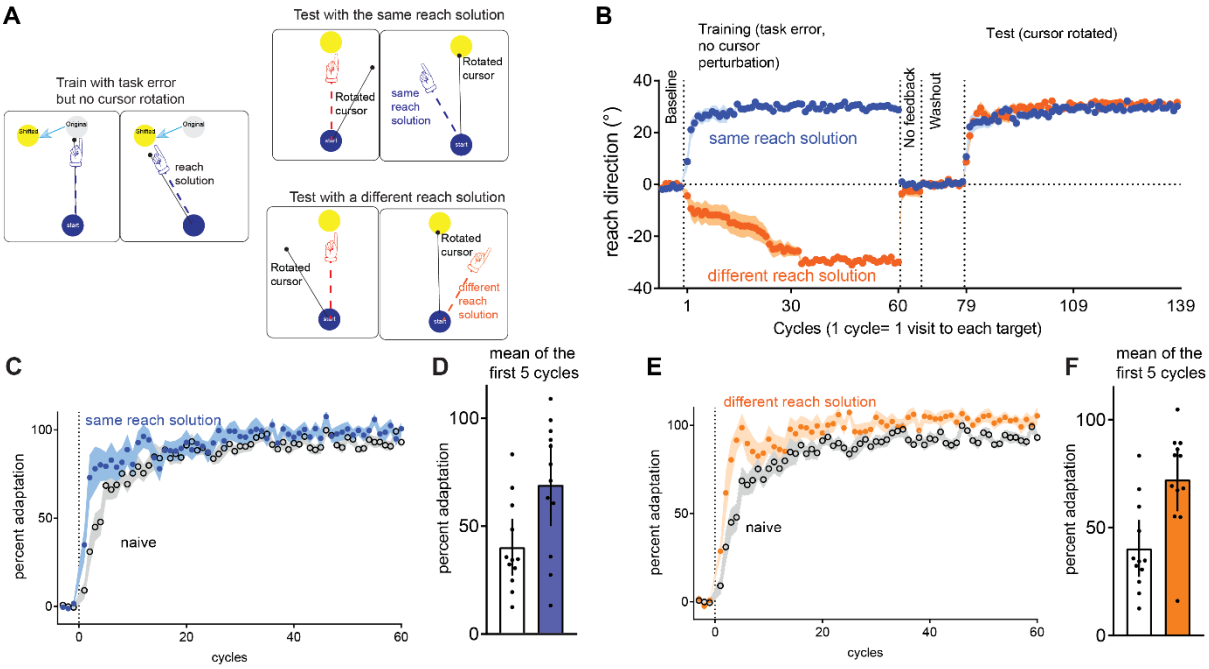

Figure 3. Experiment 3 shows that previous learning to correct for task errors in the absence of sensory prediction errors can evoke savings in visuomotor rotation. To test whether previous learning to counteract task errors could improve naive adaptation (i.e., when participants were naïve to perturbations of sensory feedback), we did not impose a cursor rotation at training, but rather moved the target away from its original position by 30° at mid-movement. To hit the target, participants had to to re-aim by 30°. Participants rapidly reverted to baseline performance after receiving instructions that all disturbances had been removed. At test, participants encountered a 30° cursor rotation for the first time. One group (Same) had the cursor rotation in the opposite direction as the target movement direction during training, such that the participants could use the same reach solution at training and test. The other group (Different) had the cursor rotation in the same direction as the target movement direction during training, such that participants had directionally opposite reach solutions at training and test. (B). Cycle-averaged reach directions throughout the experiment, where each symbol represents 1 cycle (1 visit to each target), and reaches closer to 30° during test represent reaches that more adapted. Cycle-averaged percent adaptation during test (filled circles) compared to naïve (clear circles) for the same reach solution (C) and the different reach solution (E). Mean percent adaptation averaged over the first 5 cycles with the same solution (D) and with a different solution (F) Savings was evident in more adapted reaches compared to naïve (clear symbols) for both the Same group (C & D) and the Different group (E & F). For D & F, error bars=95% CI. All other error bars are SEM.

Experiment 4: Expressing a memory of task errors at short latencies.

We next explored the mechanisms by which learning to compensate for task errors can improve subsequent visuomotor rotation adaptation. Task error correction likely relies on strategic processes that demand cognitive resources (Taylor & Thoroughman, 2007; Taylor & Thoroughman, 2008; Anguera *et al.*, 2012), because error compensation is reduced by manipulations that limit cognitive resources, such as time-constraints or a dual task (Fernandez-Ruiz *et al.*, 2011; Haith *et al.*, 2015; Leow *et al.*, 2017). These observations are consistent with the notion that mental rotation of a movement plan at a specified angle away from a target is

computationally expensive (Georgopoulos & Massey, 1987; Pellizzer & Georgopoulos, 1993; Bhat & Sanes, 1998). One can, however, learn to move at a specified angle away from a target even under time-pressure by forming some stimulus-response association between the target and required movement (McDougle & Taylor, 2019). To explore the contribution of these processes in savings, we replicated the design of Experiment 3, except that participants were required to move within a short preparation time of 250ms after the time of target presentation throughout all trials. We used the timed-response paradigm we described previously in the methods for all the previous experiments, but instead of presenting the target at 1000ms before the imperative to move, we now present the target 250ms before the imperative to move (Leow *et al.*, 2017). There were two conditions: **ShortSame** (n=12, 6 CW, 6 CCW), where the reach solution is the same at training and at test, and **ShortDifferent**, (n=12, 6 CW, 6 CCW), where the reach solution is opposite at training and at test. Cycle-averaged reach directions are shown in Figure 4. At training, despite the preparation time constraints, participants did learn to compensate for task errors (Figure 4B), as percent adaptation was larger at the late phase of the training block than the early phase.

We compared adaptation performance in the test block to a naïve control group tested under similar preparation time and task error conditions (ShortNaive, n=12, 6 CW, 6 CCW), using separate Group x Phase x Cycle ANOVAs for the ShortSame group and the ShortDifferent group. In the ShortSame group who trained with the same reach solution at test and training, adaptation at test was better than naïve (Figure 4C), significant Phase x Cycle x Group interaction, $F(10.9,240.5) = 2.01$, $p = 0.028$, partial η-squared = 0.08. Post-hoc t-tests on the mean of the first 5 cycles showed better adaptation at test 44.7+/-3.4% compared to naïve, 26.9+/-2.9%, $t(22)= 3.964$, $p=6.581e\ -4$, cohen's d=1.618).

When the reach solution at test differed from that at training in the ShortDifferent group, test performance was *worse* than naïve (Figure 4E). Phase x Group interaction, $F(1.2,26.8) = 6.92$, $p = 0.01$, partial η-squared = 0.23). Post-hoc t-tests on the mean of the first 5 cycles showed worse percent adaptation at test 11.8+/-4.4% compared to naïve: 26.9+/-2.9%, $t(22)= 2.839$, $p=0.01$, cohen's d=-1.159). This was despite the fact that subjects had already disengaged the previously learnt reach solution in the preceding no-rotation blocks with instruction (Figure 4B).

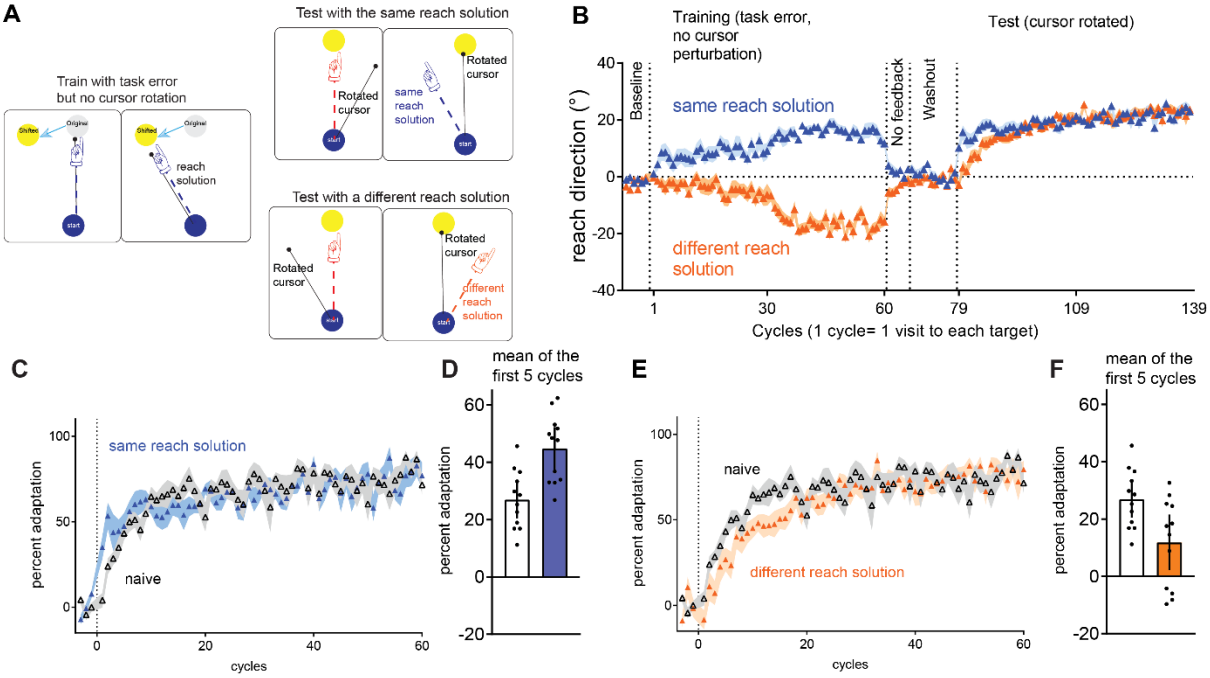

Figure 4. Experiment 4 replicates the design of Experiment 3, except that participants completed all trials under short preparation time of 250ms (A). Cycle-averaged reach directions, where each circle represents 1 cycle, or 1 visit to each target (B). Cycle-averaged percent adaptation during test (filled triangles) compared to naïve (clear triangles) for the same reach solution (C) and the different reach solution (E). Mean percent adaptation averaged over the first 5 cycles with the same solution (D) and with a different solution (F). Savings was evident in more adapted reaches compared to naïve (clear symbols) for the ShortSame group (C & D). For the ShortDifferent group, adaptation was worse than naive (E & F). For D & F, error bars=95% CI. All other error bars are SEM.

Discussion

In this work, we demonstrate a fundamental role for task errors in savings for visuomotor rotation adaptation; a phenomenon that is a hallmark of latent sensorimotor memory. We show that savings was absent without prior experience of task errors (Experiments 1 & 2), and that prior correction of task errors, even without exposure to sensory prediction errors, is sufficient to elicit savings (Experiments 3 & 4). Thus, systematic task errors that prompt adaptive motor responses can affect subsequent adaptation to never-before encountered sensorimotor perturbations. The results reinforce the notion that adaptive responses to sensorimotor perturbations take multiple forms, and suggest that task errors play a primary role in driving improved performance upon exposure to novel sensorimotor conditions. In particular, we suggest that latent sensorimotor memories which improve adaptation rely on (at least) two distinct components, both of which are driven by the failure to attain movement goals. The first is a strategic component that is flexible enough to

facilitate corrective responses in the opposite direction, but that requires substantial preparation time. The second component is a set of inflexible stimulus-response associations between targets and reach directions, that can be expressed under time-pressure.

A history of adaptation to task errors are necessary for savings

An influential model of sensorimotor adaptation suggests that a history of errors increases sensitivity to those errors, resulting in improved learning when familiar errors are re-encountered (Herzfeld *et al.*, 2014). Sensorimotor perturbations typically evoke both sensory prediction errors and task errors, but it was previously unclear how these errors contribute to latent sensorimotor memories that improve learning (Orban de Xivry & Lefevre, 2015; Leow *et al.*, 2016). Here we show that, at least in visuomotor rotation paradigms, a history of adaptation to task errors is crucial to encode latent memories that improve subsequent adaptation. Task errors that could not be corrected (i.e., enforced task errors that occurred regardless of the participants' behaviour) did not improve learning. Furthermore, Experiment 2 showed that task errors need not be present upon re-exposure to the perturbation, contradicting the proposal that task errors act as a retrieval cue to trigger savings (Huberdeau *et al.*, 2015a).

Savings do not require a history of sensory prediction errors

The results of Experiments 1 and 2 are consistent with the idea that savings results from a memory that requires task errors for its encoding. What is the nature of this learning? One possibility is that task errors drive deliberate corrective responses during adaptation (McDougle *et al.*, 2016), and that faster subsequent recognition and/ or selection of actions that correct task errors accounts for savings (Haith *et al.*, 2015; Huberdeau *et al.*, 2015a; Huberdeau *et al.*, 2015b; Morehead *et al.*, 2015). If this is true, then deliberate correction of task errors alone, even when naïve to sensory prediction errors, should be sufficient for savings. To the best of our knowledge, this question was not previously addressed (Haith *et al.*, 2015; Morehead *et al.*, 2015; Orban de Xivry & Lefevre, 2015; Huberdeau *et al.*, 2017). We therefore tested this in Experiment 3, where a systematic task error was imposed at training (targets always jumped mid-movement by 30°) without any perturbation of hand position feedback. Training to correct for these task errors improved subsequent adaptation to the 30° rotation of hand position feedback compared to

naïve participants, even though we did not provide any instruction to apply previous learning. Thus, learning to counteract task errors in the absence of a sensorimotor perturbation was enough to improve adaptation to a never-before encountered sensorimotor perturbation.

How might correction of task errors lead to savings?

Given that we can instruct participants to deliberately use re-aiming strategies to reduce errors (Mazzoni & Krakauer, 2006; Benson *et al.*, 2011; Taylor & Ivry, 2011; Schween *et al.*, 2014; Savoie *et al.*, 2018), it possible that a history of deliberately correcting for task errors leads to savings by a similar mechanism, even when the origin of errors experienced in the second exposure is different. Indeed, one view is that savings results solely from deliberate strategy use (Morehead *et al.*, 2015). This view is supported by findings of no savings when cognitive resources are suppressed by shortening movement preparation time during visuomotor adaptation (Haith *et al.*, 2015). Time pressure presumably suppresses time-consuming mental rotation processes required to re-aim at a planned angle away from the presented target (Georgopoulos & Massey, 1987; Pellizzer & Georgopoulos, 1993; Bhat & Sanes, 1998). However, it is clear than one can move at a specified angle away from a target even at short latencies (Leow *et al.*, 2017; McDougle & Taylor, 2019), and one way this might be achieved is by acquiring associations between a required movement and the target direction (i.e., via a stimulus-response association) (McDougle & Taylor, 2019). Does savings result solely from time-consuming mental rotation processes? We explored this by repeating Experiment 3 but limiting the amount of time available to prepare movements. At short latencies, improved adaptation was evident when the reach solution at test was the same as at training. When the reach solution at test was directionally opposite to the reach solution at training, participants were *worse* than naïve. We suggest that under time-pressure, learnt stimulus-response associations between target directions and the reach solution are re-expressed when participants are confronted with a similar sensorimotor context (i.e. in this case, experiencing errors to the side of targets). The learned association elicits savings when required reach solutions for each target are the same at training and test, and interference when the required reach solutions differ. This interference is particularly interesting, because it occurred despite participants being obviously able to volitionally disengage recently learned reach

solutions in the preceding no-rotation trials with similar time demands. Thus, task errors at test might have triggered retrieval of the now maladaptive reach solution, and this pre-potent response to the trigger was poorly inhibited under time pressure. We thus show that stimulus-response associations that are less amenable to volitional control also contribute to latent sensorimotor memories that alter subsequent adaptation.

Exactly what is encoded when task errors are corrected? In Experiment 3, we found that adaptive responses to task errors can be immediately switched off upon instruction that the perturbation has been removed, but that this learning was still retained in latent form to affect subsequent adaptation when a similar context was encountered. This suggests that this form of sensorimotor learning is fundamentally distinct from the adaptive responses to sensory prediction errors, which is expressed in an obligatory manner for many trials after the perturbation is removed. This persistent and obligatory response is often conceived as remapping between a desired movement direction (i.e., a motor plan) and the motor commands that are generated to achieve execute the movement. We speculate that the contextually flexible adaptive response to target errors arises from an earlier component of the sensory to motor transformation: a mapping between the behavioural goal and the motor plan selected to achieve it. This would be consistent with a non-obligatory expression of the learning, because we can choose to achieve behavioural goals in many different ways.

Athough we demonstrate a role for learning to correct task errors in improving adaptation, we do not yet fully understand *how* task errors affect learning in typical sensorimotor adaptation where task errors and sensory prediction errors co-occur. Several possibilities exist. We speculate that task errors might modulate the sensitivity to sensory prediction errors, and this increased sensitivity might elicit a gain in adaptation rate (Kim *et al.*, 2019). There is some evidence to support the second hypothesis, as task errors can modulate the alteration of sensorimotor maps as a result of exposure to sensory prediction errors (Welch, 1969; Schaefer *et al.*, 2012; Reichenthal *et al.*, 2016; Kim *et al.*, 2019). An alternative possibility is that two processes contribute independently to behaviour (1) adaptation to sensory prediction errors, and (2) implicit adaptation that is sensitive to target error (Kim *et al.*, 2019). More work is required to dissociate these possibilities.

We also do not yet understand the role of correcting task errors in adaptation to different sensorimotor perturbations which are less likely to provoke easily verbalizable strategies (e.g. force-field adaptation, split-belt treadmill adaptation) and in paradigms that are less likely to be influenced by time-consuming deliberate strategies, such as saccadic adaptation (Kojima *et al.*, 2004). It is clear that volitional strategies can influence adaptation in all of these paradigms (e.g., de'Sperati, 1999; Hwang *et al.*, 2006), but it is currently unclear to what extent strategies contribute to improved re-adaptation in these paradigms. In split-belt treadmill adaptation for example, people can strategically improve adaptation by visual feedback of their perturbation-induced gait asymmetry, and yet fail to express this improvement upon removal of visual feedback; thus failing to augment savings by explicit strategy use (Leech & Roemmich, 2018). If and how stimulus-response associations might play a role in these paradigms is even less clear.

How does the brain form latent sensorimotor memories in response to task errors and sensory prediction errors? We speculate that task errors prompt the formation of a new motor plan, which specifies the required parameters of the action required to achieve the desired outcome under new conditions. Achieving a desired outcome (e.g., a cancellation of task error) forms an association between the stimulus (e.g., task error) and the response (the movement plan). This association is readily retriggered by task errors. Learning to alter movement plans, even without actually executing the motor plan, might play a crucial role in sensorimotor adaptation (Sheahan *et al.*, 2018; Vyas *et al.*, 2018). For example, monkeys who learn to move a cursor with a brain-machine interface (i.e., without moving their hands) show accelerated adaptation when first using their hand to move a cursor (Vyas *et al.*, 2018). Similarly, although people fail to concurrently adapt to opposing perturbations, concurrent adaptation is possible when different motor plans are tagged to opposing perturbations (Sheahan *et al.*, 2018).

Summary

Our results show that failures to attain movement goals, or task errors, are a fundamental component of latent sensorimotor memories that improve adaptation to sensorimotor perturbations. Flexible, strategic processes or inflexible cached stimulus-response associations that arise in response to task errors both contribute to savings in visuomotor adaptation. The data demonstrate the richness of

behavioural responses to sensorimotor perturbations, and suggest that some principles regarding the adaptative responses to sensorimotor perturbations may be more broadly applicable to alternative motor learning contexts than previously recognised.

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