RESEARCH ARTICLE | *Control of Movement*

Practice induces a qualitative change in the memory representation for visuomotor learning

 David M. Huberdeau,[1] John W. Krakauer,[2,3]* and Adrian M. Haith[2]*

[1]*Department of Biomedical Engineering, Johns Hopkins University School of Medicine, Baltimore, Maryland;* [2]*Department of Neurology, Johns Hopkins University School of Medicine, Baltimore, Maryland; and* [3]*Department of Neuroscience, Johns Hopkins University School of Medicine, Baltimore, Maryland*

Huberdeau DM, Krakauer JW, Haith AM. Practice induces a qualitative change in the memory representation for visuomotor learning. *J Neurophysiol* 122: 1050–1059, 2019. First published August 7, 2019; doi:10.1152/jn.00830.2018.—Adaptation of our movements to changes in the environment is known to be supported by multiple learning processes that operate in parallel. One is an implicit recalibration process driven by sensory-prediction errors; the other process counters the perturbation through more deliberate compensation. Prior experience is known to enable adaptation to occur more rapidly, a phenomenon known as "savings," but exactly how experience alters each underlying learning process remains unclear. We measured the relative contributions of implicit recalibration and deliberate compensation to savings across 2 days of practice adapting to a visuomotor rotation. The rate of implicit recalibration showed no improvement with repeated practice. Instead, practice led to deliberate compensation being expressed even when preparation time was very limited. This qualitative change is consistent with the proposal that practice establishes a cached association linking target locations to appropriate motor output, facilitating a transition from deliberate to automatic action selection.

NEW & NOTEWORTHY Recent research has shown that savings for visuomotor adaptation is attributable to retrieval of intentional, strategic compensation. This does not seem consistent with the implicit nature of memory for motor skills and calls into question the validity of visuomotor adaptation of reaching movements as a model for motor skill learning. Our findings suggest a solution: that additional practice adapting to a visuomotor perturbation leads to the caching of the initially explicit strategy for countering it.

caching; explicit reaiming; learning; procedural memory

INTRODUCTION

Motor learning is often studied using adaptation tasks (Cunningham 1989; Kluzik et al. 2008; Krakauer et al. 1999, 2000; Martin et al. 1996; Shadmehr and Mussa-Ivaldi 1994; Welch et al. 1993; Wolpert et al. 1995). In these tasks, a systematic perturbation (such as a visuomotor rotation) is applied during a movement, and participants must learn to adjust their actions to cancel the effects of the perturbation and regain baseline levels of performance. The ability to adapt to an imposed perturbation is supported by at least two underlying learning processes (Huberdeau et al. 2015b). One process, implicit recalibration, uses sensory-prediction errors to recalibrate movement by adjusting the motor commands issued to reach a particular goal (Mazzoni and Krakauer 2006; Taylor et al. 2010). This process is obligatory (Mazzoni and Krakauer 2006; Morehead et al. 2015) and appears to be cerebellum-dependent (Smith and Shadmehr 2005; Tseng et al. 2007). A second process, which we refer to as deliberate compensation, corrects movement errors through more explicit means, for instance by reaiming reaching movements toward a surrogate target (McDougle and Taylor 2019; Morehead et al. 2015; Taylor et al. 2014; Werner et al. 2015).

A central question in motor learning is how prior experience affects our ability to adapt in the future. In particular, which of the two processes that contribute to adaptation is responsible for savings, i.e., the fact that adaptation is faster the second time a perturbation is encountered (Krakauer et al. 2005; Morehead et al. 2015; Zarahn et al. 2008)? Various approaches have been devised to measure the extent of implicit recalibration: one approach is to explicitly instruct participants to disengage any strategy (Benson et al. 2011; Morehead et al. 2015; Taylor et al. 2014); another approach is to limit the amount of time available to prepare a movement (Fernandez-Ruiz et al. 2011; Haith et al. 2015; Leow et al. 2017), which seems to prohibit participants from implementing time-consuming, deliberate compensation. Both approaches yield similar estimates of the relative contribution of implicit recalibration and deliberate compensation (Leow et al. 2017), and, critically, both have shown that savings is entirely attributable to deliberate compensation (Haith et al. 2015; Morehead et al. 2015; see also Hadjiosif and Smith 2013).

After a single exposure, therefore, prior experience only seems to improve future performance through time-consuming, deliberate compensation. However, a number of studies (Martin et al. 1996; Welch et al. 1993), along with everyday experience acting under perturbed mappings (e.g., using a computer mouse), suggest that people can, given enough practice, readily switch between different perturbation environments without having to engage slow, deliberate processes each time. Presumably, therefore, some aspect of adaptation must change with further practice, although it is unclear which.

* J. W. Krakauer and A. M. Haith contributed equally to this study.

Address for reprint requests and other correspondence: D. M. Huberdeau, Dept. of Psychology, Yale Univ., Box 208205, New Haven, CT 06520 (e-mail: david.huberdeau@yale.edu).

We considered two potential ways in which practice might qualitatively alter the way in which we adapt to frequently experienced perturbations. First, it has been proposed that experience may lead to an increase in the learning rate of implicit recalibration (Gonzalez Castro et al. 2014; Herzfeld et al. 2014). Although the rate of implicit recalibration appears unchanged after adapting to a perturbation once (Haith et al. 2015; Morehead et al. 2015), it is possible that repeated practice adapting and readapting to the same perturbation might bring about an increase in rate.

An alternative possibility is that implicit recalibration might remain unaffected by experience, and, instead, practice might enable initially computationally intensive deliberate compensation to be stored in the form of a cached association between target location and required motor output, allowing it to be deployed rapidly and with minimal cognitive effort (Logan 1988). Crucially, however, we would still expect that compensation that was initially deliberate could still be voluntarily disengaged even after it has become cached, and thus it would remain distinct from implicit recalibration, which is involuntary (Mazzoni and Krakauer 2006; Morehead et al. 2015). The possibility that deliberate compensation could become cached accords with long-standing theories of skill learning that posit that practice promotes a transition in representation of a skill from being deliberate to automatic (Anderson 1982; Fitts 1964), potentially through caching of time-consuming computations (Haith and Krakauer 2018).

We examined these alternatives in two experiments in which human participants adapted to a series of alternating perturbations over 2 days. We assessed implicit recalibration using Aftereffect trials in which participants were instructed to withhold any deliberate strategy and bring their (unseen) hand directly to the target (Benson et al. 2011). In parallel, we assessed how well participants were able to compensate when preparation time (PT) was severely limited (Short-PT trials; Fernandez-Ruiz et al. 2011; Haith et al. 2015; Leow et al. 2017). If practice altered the properties of implicit recalibration (increasing its rate or its asymptotic extent), then compensation during both Aftereffect trials and Short-PT trials should increase across cycles by similar magnitudes. On the other hand, if implicit recalibration remains unchanged but deliberate compensation becomes cached, the extent of compensation should improve when preparation time is limited (Short-PT trials), but there should be no change in Aftereffect trials.

MATERIALS AND METHODS

Experiment participants. Forty-one right-handed human participants with no known neurological impairments took part in this study (18–40 yr old, twenty-five women). The study was approved by the Johns Hopkins University School of Medicine Institutional Review Board, and all participants signed informed consent documents before participation.

Experimental setup. Participants were seated at a glass-surfaced table with their right forearm supported by a splint that allowed nearly frictionless planar arm movement. Participants' arms were obstructed from their own view by a mirror, on which was projected a screen from a downward-facing liquid-crystal display monitor installed above the mirror (60-Hz refresh rate).

Each participant's hand position was recorded by a Flock of Birds magnetic sensor (130 Hz; Ascension Technology, Shelburne, VT) placed under the index finger. Hand position was reported to participants via a cursor (a filled blue circle, diameter 0.5 cm) displayed on

the screen. Visual feedback of the cursor had a delay of ~100 ms (40-ms delay in the Flock of Birds and an ~60-ms delay in the visual display). Preparation time data were corrected for this delay.

Experiment 1. Twenty-one participants took part in *experiment 1* (two were later excluded from analysis; see *Data analysis* for details). Participants made rapid "shooting" movements using their right arm from a central start location (a solid green circle, diameter 1 cm) through a target (a solid light blue circle, diameter 1 cm). The target could appear at one of two locations, positioned 8 cm either to the right or left of the start location. Participants were trained to initiate their reaching movement coincident with the fourth of four audible tones (Fig. 1A). The tone sequence began 200 ms following steady placement of the cursor inside the start marker. Successive tones of 100-ms duration were played at intervals of 300 ms. On each trial, one of the two targets was presented at the onset of the first tone. During the majority of trials, the initially presented target remained on the screen either until the participant reached 9 cm radially from the start position or 2.5 s passed from the time of the first tone. Further details about different trial types are explained below.

A visuomotor perturbation in the form of a ±30° rotation of the path of the cursor relative to the start position (Fig. 1B) was applied to movements directed toward the right half of the workspace in repeating cycles throughout the experiment (Fig. 1C). Leftward-directed movements had no rotation at any time throughout the experiment. Trials with rightward-directed movements and trials with leftward-directed movements were pseudorandomly interleaved throughout each cycle so that there were 50 trials of each. Each cycle included 300 movement trials (150 trials of rightward-directed movements and 150 trials of leftward-directed movements). The rotation schedule (applied only on rightward-directed trials) was 50 trials of null rotation, 50 trials of *rotation A*, and 50 trials of *rotation B*. The direction of the cursor rotation under *rotations A* and *B* was counterbalanced across participants; in *experiment 1*, *rotation A* was a clockwise rotation for eleven participants and was a counterclockwise rotation for ten participants. Seven cycles were included across the duration of the experiment. The seventh cycle omitted *rotation B*. Two opposing rotations were used instead of alternating between a single rotation and null rotations due to the observation, in pilot experiments, that reaches made during null rotations were slow to return to baseline and retained a bias in trials in which preparation time was limited (Short-PT trials, described below) at the onset of the next cycle's rotation, making comparison across cycles problematic. Including opposing rotations ensured that behavior returned to baseline during the null rotation parts of each cycle, in all trial types.

The experiment was divided into blocks of 100 total trials (gray vertical lines in Fig. 1C), with brief breaks in between blocks. Changes in the rotation occurred in the middle of blocks, rather than coinciding with breaks between blocks. There was also an overnight break between *cycles 3* and *4* on account of the long duration of the entire experiment (which lasted ~3 h in total). It is noted, however, that overnight breaks (or sleep, more specifically) have previously been demonstrated to be important or even necessary for behavioral control to undergo some form of consolidation (Diekelmann et al. 2009; Telgen et al. 2014). Thus including an overnight break increased the chances that a potential qualitative change in memory representation would occur and be detectable.

The majority of trials in *experiment 1* were designated as long-preparation-time (Long-PT) trials. In these, the target remained in its original location for the duration of the trial so that participants had 900 ms to prepare their movement. During short-preparation-time (Short-PT) trials, the target location abruptly switched to the opposite side of the start position before the fourth tone (Fig. 1A), requiring participants to rapidly update their prepared movement. The time at which the target switched locations was randomized for each Short-PT trial by sampling from a Gaussian distribution with a mean of 300 ms and a standard deviation of 25 ms. Short-PT trials were only included during *rotation A* of the first cycle and the last cycle and,
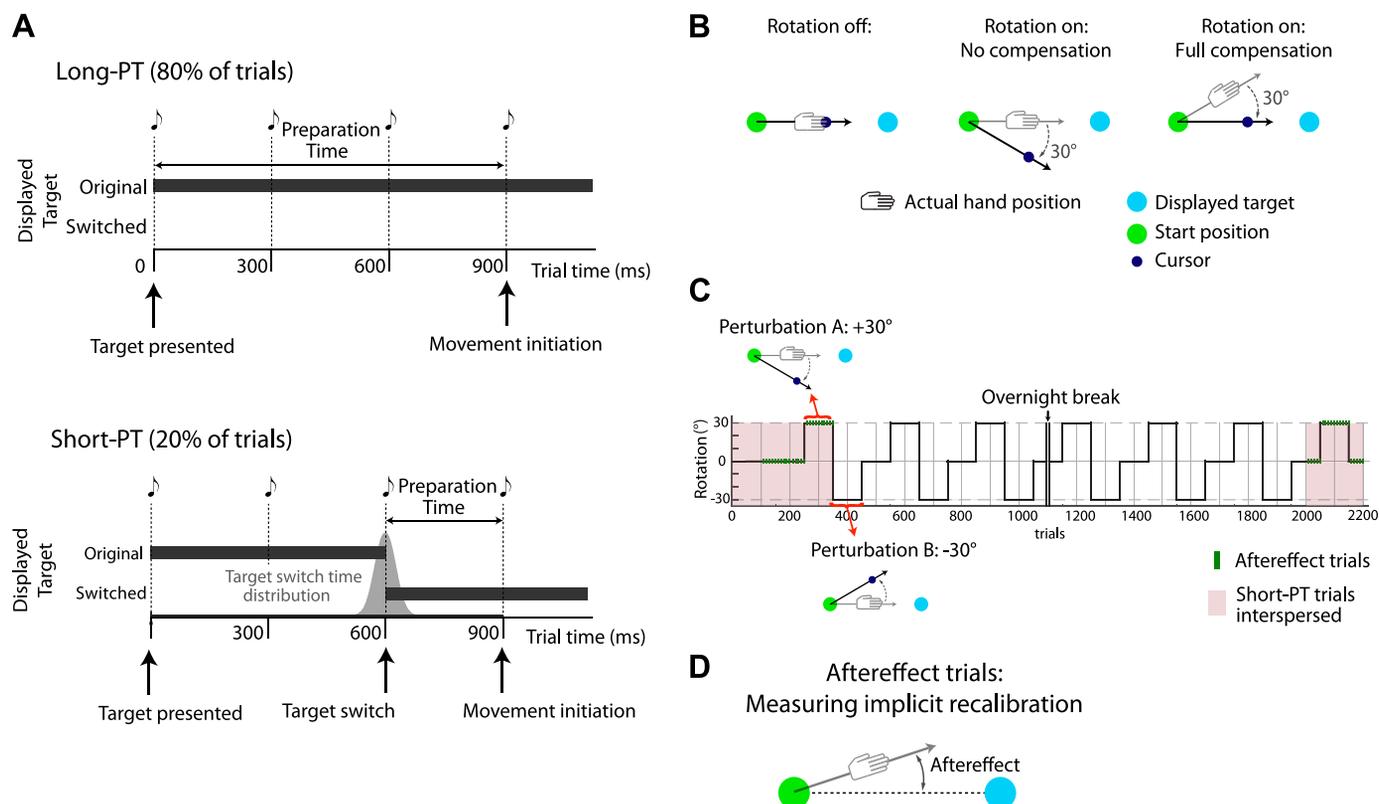
Fig. 1. Experimental design. Participants engaged in a reaching task. *A*: participants were required to initiate movement coincident with the 4th tone of a metronome. In the majority of trials (Long-PT trials; *top*), the target remained in place. In a subset of trials (Short-PT; *bottom*), the target switched locations, from left to right or from right to left, just before the 4th tone, limiting allowed preparation time. A rotation of the cursor path was imposed on the right half of the screen (*B*), and the direction of the rotation was varied in repeating cycles of 2 opposing rotation directions throughout a 2-day experiment (*C*); no rotation was imposed on the left half of the screen. Reaches to each target were pseudorandomly intermixed, with 50 trials to each target per block. *D*: Aftereffect trials, in which participants were instructed to disengage any deliberate aiming strategy and "aim directly for the target." PT, preparation time.

when present, were randomly interspersed among Long-PT trials such that for every 10 total trials, 2 were Short-PT (1 to each target) and 8 were Long-PT (4 to each target). No Short-PT trials were permitted as the 1st or last trial in each sequence of 10 trials.

In addition to Short-PT trials, Aftereffect trials (Fig. 1*D*) were included during *rotation A* of both the 1st and last rotation cycle (Fig. 1*C*). Aftereffect trials were included in all blocks in which Short-PT trials were present except for the beginning of the initial familiarization block at the outset of the experiment. Before the beginning of the experiment, participants were verbally instructed that for Aftereffect trials, they were to aim directly for the presented target, rather than applying a strategy or deliberately aiming in a direction other than toward the target (Benson et al. 2011; Day et al. 2016; Morehead et al. 2015; Werner et al. 2015). Before each Aftereffect trial, text appeared on the participant's screen for 4.5 s reading: "On the next trial / take your time / and aim directly for the target" (slashes indicate line breaks). All participants were literate in English. Participants were also verbally informed that during these Aftereffect trials, no cursor would be visible, no audible tone sequence would sound, no movement initiation time constraints were in place, and they were to reach for the target as if they wanted their finger to intersect with the target, even though they would not be able to witness this occurring. Participants were actively coached through the various trial types during an initial block of trials in which there were no rotations.

Participants were instructed to prioritize the timing of their movement initiation. They were instructed to be as accurate as possible in hitting the target with the cursor and to reach with a consistent, fast speed (between 4.5 and 13 cm/s, or movement times of 2–0.7 s over a 9-cm reach). Feedback regarding movement timing and movement speed was provided following every Long- and Short-PT trial through visual displays

on the screen (similar to Haith et al. 2015). No movement-initiation timing restrictions were imposed during Aftereffect trials, but participants tended to reach with a similar latency as in Long-PT trials (Supplemental Fig. S2; all supplemental material is available at https://doi.org/10.5281/zenodo.3273527).

Cursor feedback during the movement was provided throughout each Long- and Short-PT trial but not during Aftereffect trials. For Long- and Short-PT trials, the cursor disappeared once participants reached 9 cm radially from the start position. The cursor was not visible during the return movement until the participant's hand was within 2 cm of the start position. Any cursor manipulations (i.e., the rotations) were turned off during the intertrial period.

Experiment 2. Twenty participants took part in *experiment 2* (three were excluded from analysis due to poor performance; see *Data analysis* for details). The reaching task and rotation schedule remained the same for *experiment 2* as in *experiment 1*. *Experiment 2* included Short-PT trials throughout each rotation cycle but did not include any Aftereffect trials. *Experiment 2*, like *experiment 1*, was conducted in two sessions across 2 consecutive days. Ten participants experienced a 30° rotation of the cursor as *rotation A*, and ten experienced a −30° rotation as *rotation A*.

Data analysis. All data were analyzed offline in MATLAB (The MathWorks, Natick, MA) and in R (The R Project; https://www.r-project.org/). Kinematic data were smoothed with a second-order Savitzky-Golay interpolation filter with half-width 54 ms. These smoothed signals were then differentiated to obtain velocity. The time of movement initiation was determined by searching from the peak velocity backward in time to find the time at which tangential velocity reached a threshold of 2 cm/s. Reach direction was determined by computing the angle of the instantaneous velocity at 100 ms after

movement onset. Trials during which participants either failed to reach or abruptly altered their initial reach direction after having reached 2 cm from the start position were excluded from analysis (on average, 5 trials were excluded per participant for this reason). This type of error was most likely to have occurred during Short-PT trials, due to participants initially moving toward the original target location. Participants were excluded from further analysis if <50% of their Short-PT trials were directed toward the correct target. This led to two participants being excluded from *experiment 1* and three being excluded from *experiment 2*.

To quantify how rapidly participants adapted during a given rotation cycle, we assessed the average compensation over the first few trials of that cycle toward the perturbed target. We refer to this measure as the rate of learning. Although this measure is not a rate parameter from a model fit, it is nevertheless closely related to learning rate and thus provides a nonparametric proxy for it. We assessed this learning rate measure during Long-PT trials based on the mean reach direction over the initial eight Long-PT trials. We excluded the first trial following rotation onset and any post-Aftereffect trials from this average, however. For Short-PT trials and Aftereffect trials, the average reach direction in the initial two trials following rotation onset was taken as the rate measure for those trial types. These rate measures captured the average compensation at comparable stages of learning, i.e., given a similar number of trials since the onset of the perturbation. More trials were included to estimate average compensation for Long-PT trials compared with Short-PT and Aftereffect trials (when these were interleaved) since Long-PT outnumbered these other trial types by a ratio of 4:1. Similarly, the final eight Long-PT trials and final two Short-PT and Aftereffect trials (when these trials were present) to the perturbed target in each rotation cycle were averaged and used as a summary measure for asymptotic behavior. Long-PT trials immediately following Aftereffect trials were excluded from both rate and asymptote measures since we found that participants' behavior was systematically altered in these trials; see RESULTS for justification. Reaches directed toward the nonperturbed target had zero average error across participants and were not further analyzed.

For *experiment 1*, a mixed-effects model was fit with trial type (Long-PT, Short-PT, and Aftereffect) and rotation cycle used as factors and subjects used as random effects; a test for an interaction between trial types and rotation cycles was conducted. *t*-Tests were used to detect any difference in rate or asymptote among trial types during the first and final rotation cycles and to test for savings from the first to the final rotation cycle for each trial type. Corrections for multiple comparisons were done using the Holm method (Holm 1979).

An additional analysis was conducted to compare the structure of reaching behavior across trial types between the first and last rotation cycles of *experiment 1*. In this analysis, the reach direction of each Short-PT and Aftereffect trial was compared with the two nearest-neighboring Long-PT trials. This provided a measure of the effect of the manipulation (limiting preparation time or providing explicit instruction, respectively) compared with behavior in regular Long-PT trials. A two-way ANOVA was conducted to test whether there was an interaction in the difference between Short- and Long-PT trials and the difference between Aftereffect and Long-PT trials between the first and seventh adaptation cycle. In this analysis, cycle (*1* vs. *7*) and trial type (Short-PT vs. Aftereffect) were considered as factors. Post hoc paired *t*-tests were conducted to test for differences between the measures within each cycle and differences for each measure across cycles.

To test for savings in Short-PT trials in *experiment 2*, one-way ANOVA tests were conducted on the rate measure of Short-PT trials from each cycle. In addition, a linear mixed-effects model analysis was conducted to test for any interaction in the development of savings across cycles between Short- and Long-PT trial types. For this analysis, trial type (Long- vs. Short-PT) and cycle (for *rotation A*:

cycles *1–7*; and for *rotation B*: cycles *1–6*) were considered as fixed effects, and subject was taken as a random factor.

Preparation time data, necessary for the proper interpretation of the results, was computed for every trial by taking the difference between the time at which a reach commenced on a given trial and the time that the final target was presented. For Long-PT trials, the target did not change location, and PT was, therefore, 900 ms ± the movement-initiation timing error. For Short-PT trials, the target switched from one position to the other (as described above), and thus PT was taken as the time difference between the initiation of movement and the time of the target switch.

RESULTS

Experiment 1 sought to determine whether practice repeatedly adapting to a series of visuomotor rotations would prompt a change in the underlying representation supporting compensation. Specifically, we hypothesized that practice would lead either to a change in the properties of implicit recalibration or to caching of deliberate compensation. Participants in *experiment 1* were exposed to a repeating cycle of visuomotor rotations over 2 days (Fig. 1, *B* and *C*). In the majority of trials, participants were allowed ample time to prepare their movements (Long-PT trials), allowing for potentially time-consuming, deliberate compensation to occur (Fig. 1*A*, *top*). In contrast, a subset of trials were Short-PT trials (Fig. 1*A*, *bottom*), designed to preclude any time-consuming, deliberate components of adaptation (Fernandez-Ruiz et al. 2011; Haith et al. 2015; Leow et al. 2017) and allow only implicit recalibration and, potentially, any cached compensation (McDougle and Taylor 2019) to be expressed. In addition, we included periodic Aftereffect trials (Fig. 1*D*) in which participants were instructed to withhold any deliberate strategy, revealing the extent of implicit recalibration with no contribution from deliberate compensation, whether cached or not. Including both Short-PT trials and Aftereffect trials thus allowed us to test for cached deliberate compensation, which would be reflected in the difference in compensation between Short-PT and Aftereffect trials.

The manipulations to limit preparation time (as in Short-PT trials) and to measure the direction of reach when participants were instructed to aim directly for the target (as in Aftereffect trials) had the intended effect of limiting compensation compared with regular, Long-PT trials during the first cycle of the rotation. We established this by comparing the extent of compensation in neighboring trials of different types. Compensation was lower in Short- than in Long-PT trials during the first rotation cycle (Supplemental Fig. S1*a*, *top*; paired *t*-test: $t = 5.97$, $P < 0.001$). Compensation in Aftereffect trials was also lower than in Long-PT trials (Supplemental Fig. S1*a*, *top*; paired *t*-test: $t = 4.92$, $P < 0.001$). We also conducted an analysis of variance to quantify the extent to which probe trial types were similar in their difference compared with the Long-PT trials. There was no evidence for such a difference in *cycle 1* [ANOVA: $F(1, 30) = 2.28$, $P = 0.142$].

Participants were able to adapt to the alternating rotation (Fig. 2*A*) and appeared to exhibit savings in both Long- and Short-PT trials across cycles (Fig. 2, *B* and *C*) but not in Aftereffect trials. To evaluate this statistically, we used a mixed-effects model to test for any interaction among trial types across cycles and then post hoc tests in the event of an interaction to test for savings in each trial type individually.
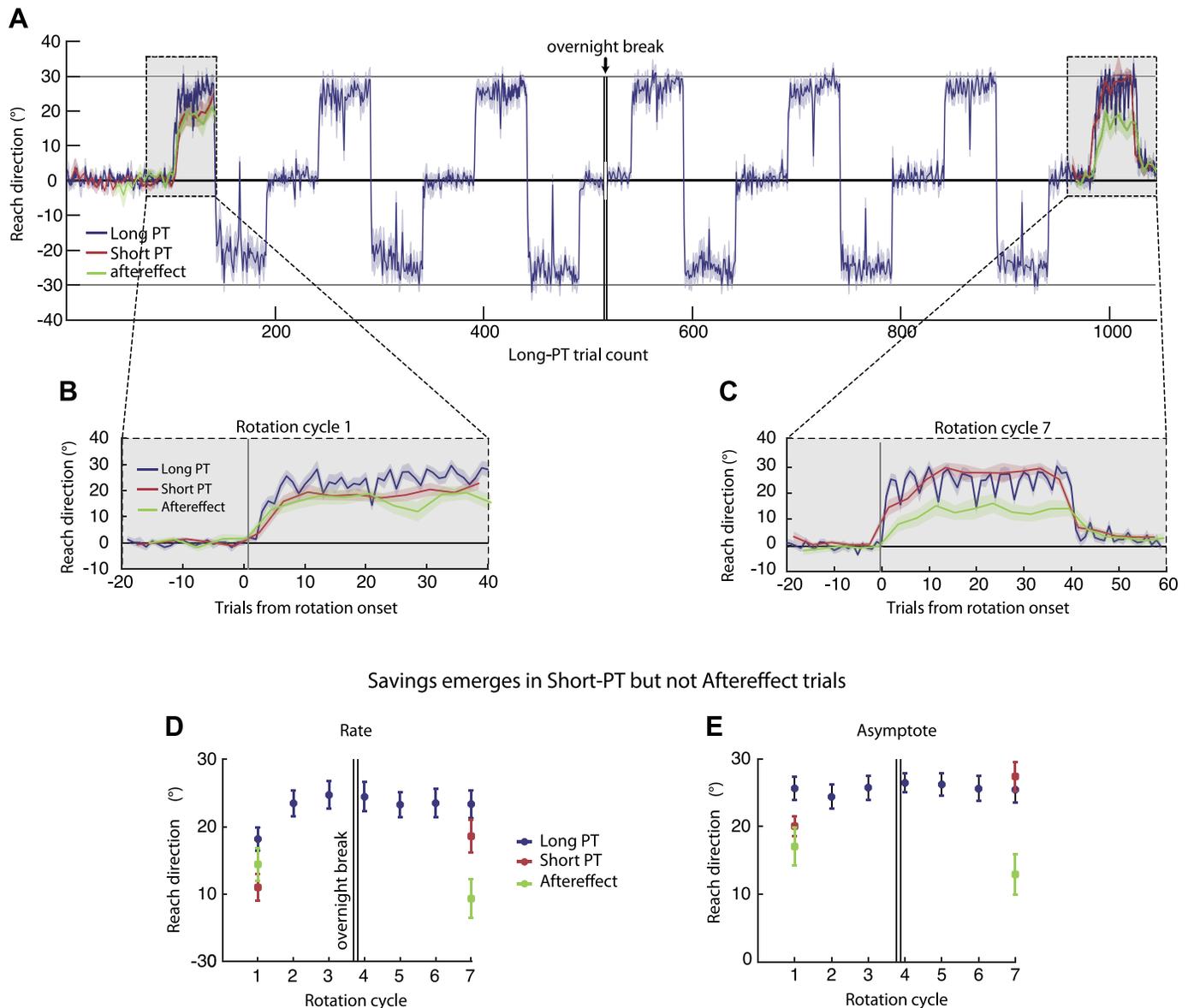
Fig. 2. *Experiment 1* results. *A*: mean reach direction ($\pm$ SE) across participants throughout the whole experiment. Blue, Long-PT trials; red, Short-PT trials; green, Aftereffect trials. *B*: enlarged view of mean behavior during *cycle 1*. *C*: enlarged view of mean behavior during *cycle 7*. *D*: extent of compensation early after perturbation onset for each cycle. *E*: as *D* but showing asymptotic compensation within each cycle. Error bars represent $\pm$ SE. PT, preparation time.

There was a significant interaction between cycles and trial types in the measure of learning rate, indicating that trial types exhibited different changes in learning rate across cycles [$\chi^2(2) = 16.2$, $P < 0.001$]. As expected, across repeated bouts of adaptation, participants became able to compensate more rapidly in Long-PT trials (*rotation A, cycle 7* vs. *cycle 1*: $t = 4.24$, $P < 0.001$; *rotation B*: $t = 3.88$, $P < 0.01$). This improvement was not attributable to differences in baseline at the start of each cycle, which was well-matched across cycles for all 3 trial types (1st vs. last cycle; Long-PT: $t = 0.687$, $P = 0.50$; Short-PT: $t = 0.0253$, $P = 0.98$; and Aftereffect: $t = 0.366$, $P = 0.72$). Short-PT trials also exhibited savings (Fig. 2, *D* and *E*; paired *t*-tests: rate: $t = 2.84$, $P < 0.05$; asymptote: $t = 5.23$, $P < 0.001$). However, Aftereffect trials did not exhibit savings, showing instead a slight reduction in adaptation rate during the seventh cycle compared with the first cycle [Fig. 2, *D* and *E*; rate: effect size (mean $\pm$ standard

error) $= 5.3 \pm 2.5°$; $t = 2.08$, $P = 0.052$; asymptote: effect size (mean $\pm$ standard error) $= 4.5 \pm 1.8°$, $t = 2.48$, $P < 0.05$]. Thus changes in implicit recalibration could not account for the savings expressed in Long- and Short-PT trials.

This was further supported by an analysis of the difference in the extent of compensation between neighboring trials of different type: a 2-way analysis of variance on the difference in reach direction between adjacent Long- and Short-PT trials and between adjacent Long-PT and Aftereffect trials showed a significant effect of trial type and a significant trial-type-by-cycle interaction [Supplemental Fig. S1*b*; 2-way ANOVA: trial type: $F(1, 56) = 17.7$, $P < 0.01$; cycle: $F(1, 56) = 0.001$, $P = 0.98$; interaction: $F(1, 56) = 7.63$, $P < 0.01$].

In summary, we found that implicit recalibration did not become more sensitive to error despite extensive practice adapting to a visuomotor rotation, i.e., the rate of adaptation appeared to remain constant despite participants having exten-

sive experience adapting to the perturbation. Practice did, however, lead to a change in deliberate compensation, apparent in the fact that, by the seventh cycle, participants had become able to compensate more completely in Short-PT trials, when preparation time was limited. This is consistent with a transition from a computationally expensive process to one that was cached.

The conclusions from the measure of rate were recapitulated in the asymptote measure. The change in the extent of adaptation at asymptote was different for the three trials types, evidenced by a significant interaction [Fig. 2E; mixed-effects model: $\chi^2(2) = 27.0$, $P < 0.001$]. There was a significant increase in Short-PT trials (paired t-test: $t = 4.82$, $P < 0.01$) but a significant drop in Aftereffect trials (paired t-test: $t = -2.63$, $P = 0.042$), consistent with there being a change in representation for the deliberate component to adaptation rather than a change in the properties of implicit recalibration. Long-PT trials did not sig-

nificantly differ between the first and last cycle at asymptote (paired t-test: $t = -0.84$, $P = 0.42$).

Savings at low latency emerged gradually and for both perturbation directions. The results of *experiment 1* showed that repeated exposure to a perturbation led to a qualitative change in the nature of the memory supporting savings, with more complete compensation to the rotation being able to be expressed under limited preparation time following practice (Fig. 2A). *Experiment 2* sought to further explore this transition by including Short-PT trials throughout the practice period to probe the time course of this change. Furthermore, we also included Short-PT trials for *rotation B* (in addition to *rotation A*). *Experiment 2* confirmed the key finding from *experiment 1*: that savings became expressible at short latency following practice (Fig. 3A). An analysis of variance test conducted on the rate measure from Short-PT trials under *rotation A* (Fig. 3B) confirmed that the rates differed across cycles [ANOVA: $F(1, 105) = 11.44$, $P < 0.01$]. This was also true for the
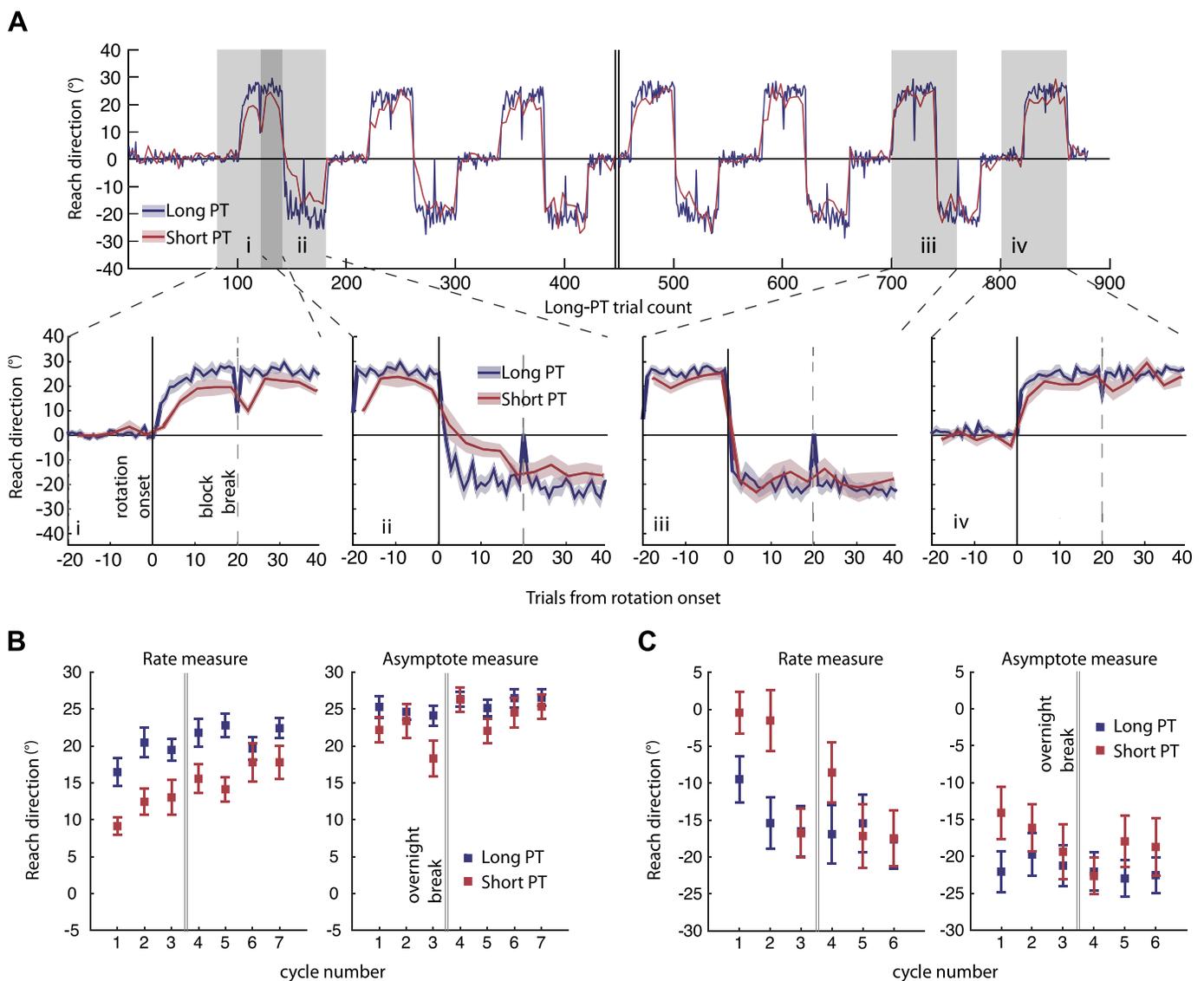
Fig. 3. *Experiment 2* results. *A*: mean reach direction (± SE) across participants. Blue, Long-PT trials; red, Short-PT trials. *Bottom* shows enlarged view of behavior during the onset of *perturbation A* during *cycle 1* (*i*), the transition from *perturbation A* to *B* during *cycle 1* (*ii*), the last transition from *perturbation A* to *B*, which occurred in *cycle 6* (*iii*), and the onset of *perturbation A* in *cycle 7* (*iv*). *B*: mean performance across cycles for Long-PT (blue) and Short-PT (red) trials. *Left*: rate measure for *perturbation A*. *Right*: asymptote measure for *perturbation A*. *C*: as in *B* but for *perturbation B*. PT, preparation time.

rate measures from *rotation B* [Fig. 3*C*; ANOVA: $F(1, 82) = 11.23$, $P < 0.01$].

To determine whether savings developed differently in Short-PT trials compared with Long-PT trials, we conducted a linear two-way mixed-effects analysis that included data from all available cycles of *rotation A*. Although this analysis was unable to detect a reliable interaction [Fig. 3*B*; cycle-by-trial-type interaction for rate: $\chi^2(1) = 1.95$, $P = 0.16$; and for asymptote: $\chi^2(1) = 0.27$, $P = 0.60$], it did detect a significant effect marginally across cycles [mixed-effects regression: cycle: $\chi^2(1) = 22.7$, $P < 0.001$], confirming that savings changed with practice. Behavior under *rotation B* did, however, reveal a clear difference between savings expressed in Short- and Long-PT trials; behavior in Long-PT trials seemed to change little after the second cycle, whereas behavior in Short-PT trials continued to change across cycles (Fig. 3*C*). This was confirmed by a mixed-effects cycle-by-trial-type interaction [$\chi^2(1) = 14.3$, $P < 0.001$], with significant savings across cycles [cycle: $\chi^2(1) = 44.5$, $P < 0.001$]. Thus, for *rotation B*, the emergence of savings followed different time courses for Short-PT trials and Long-PT trials.

DISCUSSION

We sought to establish how practice affected each of the two learning processes that are known to support our ability to compensate for an imposed perturbation. *Experiment 1* clearly demonstrated that repeated practice adapting to a perturbation did not lead to an increase in the rate of implicit adaptation. Practice did, however, lead to a change in the ability to apply deliberate compensation. With practice, participants were able to compensate for the rotation even when preparation time was limited. *Experiment 2* replicated this effect and extended our conclusions by showing that savings in trials in which reaction time was limited (i.e., Short-PT trials) emerged gradually with practice and followed a dissociable time course from savings seen when ample preparation time was available (i.e., in Long-PT trials).

We included cycles of opposing visuomotor rotations to ensure that reaching behavior returned to baseline in between cycles. However, this manipulation might also have slowed adaptation during each rotation through an interference effect (Krakauer et al. 2005). Indeed, adaptation did appear to reach a lower asymptote compared with similar previous experiments (Haith et al. 2015). Despite the possible blunting effects of interference, we still observed robust savings across cycles in Long- and Short-PT trials, consistent with previous findings examining structural learning (Turnham et al. 2012). It is possible that the opposing rotations might have blunted possible savings for implicit recalibration. If anything, however, previous theories of savings couched at the level of implicit recalibration suggest that the learning rate ought to increase in our experiment due to the high environmental consistency (Gonzalez Castro et al. 2014) and distinct pattern of errors experienced each time the perturbation changed (Herzfeld et al. 2014). Interference effects in adaptation paradigms have largely been attributed to a cognitive failure to retrieve a previously learned solution (Krakauer et al. 2005; Yin and Wei 2014). We speculate that the transition to a cached representation through practice may have helped to overcome such interference effects.

If savings cannot be attributed to a change in the rate of implicit recalibration, other components of adaptation must be responsible. We have previously argued that savings comes about through a mechanism of retrieval of previously successful actions or strategies when a perturbation is experienced again (Huang et al. 2011; Huberdeau et al. 2015a). Savings after adaptation to a single session of exposure to a perturbation is attributable to retrieval of a specific reaiming strategy (Huberdeau et al. 2015a; Morehead et al. 2015). This retrieval explanation for savings could also be consistent with an explanation for savings in terms of memory for errors (Huberdeau et al. 2015a) if a specific error acts as a cue for retrieval. Our findings suggest that the retrieved solution was time consuming to implement initially (Haith et al. 2015), but repeated practice enabled it to be applied at short latency. One possible mechanism by which this might happen is that participants underwent a qualitative change from retrieving an explicit reaiming strategy to retrieving a more direct association between targets and required reach directions (McDougle and Taylor 2018), which could be implemented more rapidly.

It is also possible that the change in representation that allowed retrieval at lower latencies was parametric, rather than qualitative. For instance, practice might have reduced the uncertainty about what compensatory behavior canceled the rotation, and the reduced uncertainty enabled more precise recall at lower latencies. In either case, however, retrieval of the appropriate reach direction was achieved in fewer trials and at low preparation times only after repeated exposure to cycles of the rotation, demonstrating a longer-term practice effect. Regardless of the specific underlying mechanism, these results are consistent with previous work showing that memory retrieval improves with practice (Karpicke and Roediger 2008; Rickard and Bajic 2006).

It has also been suggested that the mechanism for the deliberate component of adaptation might involve mental rotation to compute a required reaiming location (Fernandez-Ruiz et al. 2011; McDougle and Taylor 2019). This idea would also be consistent with our findings, as mental rotation is known to be time consuming (Shepard and Metzler 1971). Furthermore, mental rotation has been found to undergo a change in representation with practice (Logan 1988; Provost et al. 2013), consistent with the idea that practice enables a direct, cached stimulus-response association to be established, similar to the qualitative change that we propose occurs here for savings. This same argument would apply for other potential processes by which the solution to the rotation might be initially represented. For example, if the reach direction that fully counteracts the perturbation were memorized in some explicit way, e.g., through the use of labeled numbers along an arc (Taylor et al. 2014), this would also likely require additional processing time to apply, which could be sped up through practice by a similar caching mechanism.

Practice is known to lead to a variety of effects on behavior. In addition to enabling more rapid processing, it also enables skills to be performed with fewer cognitive resources. However, extensive practice also leads to behavior that is less flexible, i.e., habitual. Some or all of these practice-related changes in behavior are often described in terms of a transition to automatic behavior (Hélie and Cousineau 2011; Logan 1985; Shiffrin and Dumais 1981; Shiffrin and Schneider 1977), and each is broadly consistent with the idea that automaticity

reflects a transition to a cached representation (Haith and Krakauer 2018). In a recent study, Hardwick and colleagues (2017) showed that, in an arbitrary visuomotor association task, practice improved the ability to respond appropriately under time pressure, as in our results here. Furthermore, the improved responsiveness was associated with emergence of habitual responding, i.e., after stimulus-response contingencies were changed, participants persisted in making responses consistent with the old contingency, providing evidence of a qualitative change in the underlying representation. In our present experiments, participants showed clear improvements in the speed of processing but were also able to flexibly switch to a different cached mapping each time the perturbation changed, suggesting a possible dissociation between different facets of automaticity. However, the ability to switch to an alternate cached association is likely also practice-dependent. It remains uncertain exactly how different characteristics of automaticity are related to one another (Haith and Krakauer 2018).

How can patients with amnesia learn new motor skills that rely on recall? Despite severe anterograde amnesia, H.M. and other patients like him are capable of learning novel motor abilities like mirror drawing, with no recollection of ever having done the task (Cohen and Squire 1980; Milner 1962). These findings directly gave rise to the notion that motor skills are procedural and distinct from declarative memory (Cohen and Squire 1980). How can the H.M. result be reconciled with our model of a transformation from deliberate to cached behavior? We suggest that the processes needed for deliberate behavior are, in fact, intact in amnesic patients (Schacter et al. 1982; Squire and Zola 1998; Tulving 1985), even though the ability to build long-term memories for these processes is impaired (Stanley and Krakauer 2013). Thus individuals with amnesia could have been able to gradually learn new skills by caching fragments of deliberate behavior within each session of practice. Iterating this fragmentary process could ultimately allow a new, cached association mediating a newly learned skill to be gradually acquired and retained across sessions, even though the skill initially depended on deliberate processes.

Relationship between adaptation and motor skill learning. Our finding that practice had little effect on the properties of implicit recalibration casts doubt on the idea that the learning mechanisms responsible for implicit recalibration might also play an integral role in more general long-term skill learning. The relationship of simple adaptation tasks to more complex real-world skills is questionable (Krakauer et al. 2019; Krakauer and Mazzoni 2011; Wolpert et al. 2011; Wulf and Shea 2002) as, unlike typical skills, the timescale of adaptation learning is rapid (Mazzoni and Krakauer 2006). Furthermore, adaptation is a transient state that, unlike other skills, tends to deteriorate rather than consolidate with the passage of time (Kitago et al. 2013; Telgen et al. 2014).

Implicit motor learning in humans has been strongly linked to the cerebellum (Bastian 2006; Butcher et al. 2017; Huberdeau et al. 2015b; Taylor et al. 2010), and the cerebellum has often been implicated in the acquisition of long-term skills through practice (Doyon et al. 2003; Hikosaka et al. 2002). However, we suggest that any role the cerebellum has in long-term skill acquisition is unlikely to occur through its capacity to recalibrate movement in response to movement errors. Prior work has instead suggested that the cerebellum may be necessary for other computations that contribute to long-term motor learning, such as in establishing automatic behavioral responses. Functional imaging studies in humans suggest that neural activity in the cerebellar regions Crus I and II correlate with the automatization of behavior (Balsters and Ramnani 2011). Intriguingly, lesions of the cerebellum that include these same regions in nonhuman primates disrupt the ability to perform overlearned compensation for prisms that displace the visual field (Baizer et al. 1999; Norris et al. 2011); similar lesions restricted to cerebellum lobules V and VI/VII, regions typically implicated in implicit recalibration, had little effect on overlearned compensation (Baizer et al. 1999; Norris et al. 2011).

Our present findings show how a deliberate compensatory strategy that is initially computationally expensive can become cached following practice, enabling it to be deployed rapidly. This transition is directly comparable with the transition from declarative to procedural memory that has commonly been invoked in theories of skill learning (Anderson 1982; Fitts and Posner 1967). Thus, in a restricted sense, adaptation paradigms do encompass a model of more general skill-learning processes. Nevertheless, the presence of implicit recalibration, which appears to be insensitive to practice-related effects, significantly complicates the skill-related phenomena in such paradigms. We suggest that skill learning might be better studied in paradigms that more effectively isolate the deliberate-to-cached transition.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.M.H., J.W.K., and A.M.H. conceived and designed research; D.M.H. performed experiments; D.M.H. analyzed data; D.M.H., J.W.K., and A.M.H. interpreted results of experiments; D.M.H. prepared figures; D.M.H. drafted manuscript; D.M.H., J.W.K., and A.M.H. edited and revised manuscript; J.W.K. and A.M.H. approved final version of manuscript.

REFERENCES

Anderson JR. Acquisition of cognitive skill. *Psychol Rev* 89: 369–406, 1982. doi:10.1037/0033-295X.89.4.369.

Baizer JS, Kralj-Hans I, Glickstein M. Cerebellar lesions and prism adaptation in macaque monkeys. *J Neurophysiol* 81: 1960–1965, 1999. doi:10.1152/jn.1999.81.4.1960.

Balsters JH, Ramnani N. Cerebellar plasticity and the automation of first-order rules. *J Neurosci* 31: 2305–2312, 2011. doi:10.1523/JNEUROSCI.4358-10.2011.

Bastian AJ. Learning to predict the future: the cerebellum adapts feedforward movement control. *Curr Opin Neurobiol* 16: 645–649, 2006. doi:10.1016/j.conb.2006.08.016.

Benson BL, Anguera JA, Seidler RD. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J Neurophysiol* 105: 2843–2851, 2011. doi:10.1152/jn.00002.2011.

Butcher PA, Ivry RB, Kuo SH, Rydz D, Krakauer JW, Taylor JA. The cerebellum does more than sensory prediction error-based learning in sensorimotor adaptation tasks. *J Neurophysiol* 118: 1622–1636, 2017. doi:10.1152/jn.00451.2017.

Cohen NJ, Squire LR. Preserved learning and retention of pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. *Science* 210: 207–210, 1980. doi:10.1126/science.7414331.

Cunningham HA. Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *J Exp Psychol Hum Percept Perform* 15: 493–506, 1989. doi:10.1037/0096-1523.15.3.493.

Day KA, Roemmich RT, Taylor JA, Bastian AJ. Visuomotor learning generalizes around the intended movement. *eNeuro* 3: ENEURO.0005-16.2016, 2016. doi:10.1523/ENEURO.0005-16.2016.

Diekelmann S, Wilhelm I, Born J. The whats and whens of sleep-dependent memory consolidation. *Sleep Med Rev* 13: 309–321, 2009. doi:10.1016/j.smrv.2008.08.002.

Doyon J, Penhune V, Ungerleider LG. Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia* 41: 252–262, 2003. doi:10.1016/S0028-3932(02)00158-6.

Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan JR. Relation between reaction time and reach errors during visuomotor adaptation. *Behav Brain Res* 219: 8–14, 2011. doi:10.1016/j.bbr.2010.11.060.

Fitts PM. Perceptual motor skill learning. In: *Categories of Human Learning*, edited by Melton AW. New York: Academic, 1964, p. 244–283.

Fitts PM, Posner MI. *Human Performance*. Belmont, CA: Brooks-Cole, 1967.

Gonzalez Castro LN, Hadjiosif AM, Hemphill MA, Smith MA. Environmental consistency determines the rate of motor adaptation. *Curr Biol* 24: 1050–1061, 2014. doi:10.1016/j.cub.2014.03.049.

Hadjiosif A, Smith MA. Savings is restricted to the temporally labile component of motor adaptation (Abstract). *Translational and Computational Motor Control*. San Diego, CA, November 8, 2013, p. 409–419.

Haith AM, Huberdeau DM, Krakauer JW. The influence of movement preparation time on the expression of visuomotor learning and savings. *J Neurosci* 35: 5109–5117, 2015. doi:10.1523/JNEUROSCI.3869-14.2015.

Haith AM, Krakauer JW. The multiple effects of practice: skill, habit and reduced cognitive load. *Curr Opin Behav Sci* 20: 196–201, 2018. doi:10.1016/j.cobeha.2018.01.015.

Hardwick RM, Forrence AD, Krakauer JW, Haith AM. Skill acquisition and habit formation as distinct effects of practice (Preprint). *bioRxiv* 201095, 2017. doi:10.1101/201095.

Hélie S, Cousineau D. The cognitive neuroscience of automaticity: behavioral and brain signatures. *Cogn Sci (Hauppauge)* 6: 35–53, 2011.

Herzfeld DJ, Vaswani PA, Marko MK, Shadmehr R. A memory of errors in sensorimotor learning. *Science* 345: 1349–1353, 2014. doi:10.1126/science.1253138.

Hikosaka O, Nakamura K, Sakai K, Nakahara H. Central mechanisms of motor skill learning. *Curr Opin Neurobiol* 12: 217–222, 2002. doi:10.1016/S0959-4388(02)00307-0.

Holm S. A simple sequentially rejective multiple test procedure. *Scand Stat Theory Appl* 6: 65–70, 1979.

Huang VS, Haith A, Mazzoni P, Krakauer JW. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* 70: 787–801, 2011. doi:10.1016/j.neuron.2011.04.012.

Huberdeau DM, Haith AM, Krakauer JW. Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *J Neurophysiol* 114: 969–977, 2015a. doi:10.1152/jn.00369.2015.

Huberdeau DM, Krakauer JW, Haith AM. Dual-process decomposition in human sensorimotor adaptation. *Curr Opin Neurobiol* 33: 71–77, 2015b. doi:10.1016/j.conb.2015.03.003.

Karpicke JD, Roediger HL 3rd. The critical importance of retrieval for learning. *Science* 319: 966–968, 2008. doi:10.1126/science.1152408.

Kitago T, Ryan SL, Mazzoni P, Krakauer JW, Haith AM. Unlearning versus savings in visuomotor adaptation: comparing effects of washout, passage of time, and removal of errors on motor memory. *Front Hum Neurosci* 7: 307, 2013. doi:10.3389/fnhum.2013.00307.

Kluzik J, Diedrichsen J, Shadmehr R, Bastian AJ. Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? *J Neurophysiol* 100: 1455–1464, 2008. doi:10.1152/jn.90334.2008.

Krakauer JW, Ghez C, Ghilardi MF. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci* 25: 473–478, 2005. doi:10.1523/JNEUROSCI.4218-04.2005.

Krakauer JW, Ghilardi MF, Ghez C. Independent learning of internal models for kinematic and dynamic control of reaching. *Nat Neurosci* 2: 1026–1031, 1999. doi:10.1038/14826.

Krakauer JW, Hadjiosif AM, Xu J, Wong AL, Haith AM. Motor learning. *Compr Physiol* 9: 613–663, 2019. doi:10.1002/cphy.c170043.

Krakauer JW, Mazzoni P. Human sensorimotor learning: adaptation, skill, and beyond. *Curr Opin Neurobiol* 21: 636–644, 2011. doi:10.1016/j.conb.2011.06.012.

Krakauer JW, Pine ZM, Ghilardi MF, Ghez C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000. doi:10.1523/JNEUROSCI.20-23-08916.2000.

Leow LA, Gunn R, Marinovic W, Carroll TJ. Estimating the implicit component of visuomotor rotation learning by constraining movement preparation time. *J Neurophysiol* 118: 666–676, 2017. doi:10.1152/jn.00834.2016.

Logan GD. Skill and automaticity: relations, implications, and future directions. *Can J Psychol* 39: 367–386, 1985. doi:10.1037/h0080066.

Logan GD. Toward an instance theory of automatization. *Psychol Rev* 95: 492–527, 1988. doi:10.1037/0033-295X.95.4.492.

Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT. Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119: 1199–1211, 1996. doi:10.1093/brain/119.4.1199.

Mazzoni P, Krakauer JW. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci* 26: 3642–3645, 2006. doi:10.1523/JNEUROSCI.5317-05.2006.

McDougle SD, Taylor JA. Dissociable cognitive strategies for sensorimotor learning. *Nat Commun* 10: 40, 2019. doi:10.1038/s41467-018-07941-0.

McDougle SD, Taylor JA. Dissociable roles for working memory in sensorimotor learning (Preprint). *bioRxiv* 290189, 2018. doi:10.1101/290189.

Milner B. Les troubles de la memoire accompagnant des lesions hippocampiques bilaterales. In: *Physiologie de l'Hippocampe*. Paris: Centre National de la Recherche Scientifique, 1962, p. 257–272.

Morehead JR, Qasim SE, Crossley MJ, Ivry R. Savings upon re-aiming in visuomotor adaptation. *J Neurosci* 35: 14386–14396, 2015. doi:10.1523/JNEUROSCI.1046-15.2015.

Norris SA, Hathaway EN, Taylor JA, Thach WT. Cerebellar inactivation impairs memory of learned prism gaze-reach calibrations. *J Neurophysiol* 105: 2248–2259, 2011. doi:10.1152/jn.01009.2010.

Provost A, Johnson B, Karayanidis F, Brown SD, Heathcote A. Two routes to expertise in mental rotation. *Cogn Sci* 37: 1321–1342, 2013. doi:10.1111/cogs.12042.

Rickard TC, Bajic D. Cued recall from image and sentence memory: a shift from episodic to identical elements representation. *J Exp Psychol Learn Mem Cogn* 32: 734–748, 2006. doi:10.1037/0278-7393.32.4.734.

Schacter DL, Wang PL, Tulving E, Freedman M. Functional retrograde amnesia: a quantitative case study. *Neuropsychologia* 20: 523–532, 1982. doi:10.1016/0028-3932(82)90026-4.

Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994. doi:10.1523/JNEUROSCI.14-05-03208.1994.

Shepard RN, Metzler J. Mental rotation of three-dimensional objects. *Science* 171: 701–703, 1971. doi:10.1126/science.171.3972.701.

Shiffrin RM, Dumais ST. The development of automatism. In: *Cognitive Skills and Their Acquisition*, edited by Anderson JR. New York: Taylor & Francis, 1981, p. 111–140. doi:10.4324/9780203728178.

Shiffrin RM, Schneider W. Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychol Rev* 84: 127–190, 1977. doi:10.1037/0033-295X.84.2.127.

Smith MA, Shadmehr R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J Neurophysiol* 93: 2809–2821, 2005. doi:10.1152/jn.00943.2004.

Squire LR, Zola SM. Episodic memory, semantic memory, and amnesia. *Hippocampus* 8: 205–211, 1998. doi:10.1002/(SICI)1098-1063(1998)8:3<205:AID-HIPO3>3.0.CO;2-I.

Stanley J, Krakauer JW. Motor skill depends on knowledge of facts. *Front Hum Neurosci* 7: 503, 2013. doi:10.3389/fnhum.2013.00503.

Taylor JA, Klemfuss NM, Ivry RB. An explicit strategy prevails when the cerebellum fails to compute movement errors. *Cerebellum* 9: 580–586, 2010. doi:10.1007/s12311-010-0201-x.

Taylor JA, Krakauer JW, Ivry RB. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci* 34: 3023–3032, 2014. doi:10.1523/JNEUROSCI.3619-13.2014.

Telgen S, Parvin D, Diedrichsen J. Mirror reversal and visual rotation are learned and consolidated via separate mechanisms: recalibrating or learning de novo? *J Neurosci* 34: 13768–13779, 2014. doi:10.1523/JNEUROSCI.5306-13.2014.

Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 98: 54–62, 2007. doi:10.1152/jn.00266.2007.

Tulving E. Memory and consciousness. *Can Psychol* 26: 1–12, 1985. doi:10.1037/h0080017.

Turnham E, Braun DA, Wolpert DM. Facilitation of learning induced by both random and gradual visuomotor task variation. *J Neurophysiol* 107: 1111–1122, 2012. doi:10.1152/jn.00635.2011.

Welch RB, Bridgeman B, Anand S, Browman KE. Alternating prism exposure causes dual adaptation and generalization to a novel displacement. *Percept Psychophys* 54: 195–204, 1993. doi:10.3758/BF03211756.

Werner S, van Aken BC, Hulst T, Frens MA, van der Geest JN, Strüder HK, Donchin O. Awareness of sensorimotor adaptation to visual rotations of different size. *PLoS One* 10: e0123321, 2015. doi:10.1371/journal.pone.0123321.

Wolpert DM, Diedrichsen J, Flanagan JR. Principles of sensorimotor learning. *Nat Rev Neurosci* 12: 739–751, 2011. doi:10.1038/nrn3112.

Wolpert DM, Ghahramani Z, Jordan MI. An internal model for sensorimotor integration. *Science* 269: 1880–1882, 1995. doi:10.1126/science.7569931.

Wulf G, Shea CH. Principles derived from the study of simple skills do not generalize to complex skill learning. *Psychon Bull Rev* 9: 185–211, 2002. doi:10.3758/BF03196276.

Yin C, Wei K. Interference from mere thinking: mental rehearsal temporarily disrupts recall of motor memory. *J Neurophysiol* 112: 594–602, 2014. doi:10.1152/jn.00070.2014.

Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW. Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J Neurophysiol* 100: 2537–2548, 2008. doi:10.1152/jn.90529.2008.