Explicit and Implicit Processes Exhibit Opposite Effects Upon Relearning a Sensorimotor Perturbation

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Savings-upon-relearning, a core memory phenomenon encompassed in many theories of learning, has been the subject of considerable debate in the realm of motor learning. In recent work on visuomotor adaptation, the majority of savings has been shown to arise from the explicit recall of appropriate compensatory strategies used to counteract a previously experienced perturbation (Morehead *et al*., 2015). Whether implicit adaptation also contributes to savings remains unclear: Some studies have reported savings on measures associated with implicit adaptation when a perturbation is re-experienced (Coltman *et al.* 2019; Yin and Wei 2020), whereas other studies reported that this component of learning does not exhibit savings (Haith *et al.*, 2015; Morehead *et al.*, 2015; Leow *et al.*, 2020). We revisit this question in the present set of experiments, using a set of methods that have been shown to isolate the contribution of implicit adaptation to performance.

In Experiment 1, we modified a task that assays, in parallel, the contributions of explicit and implicit processes to savings in a visuomotor rotation task (Morehead *et al.*, 2015). Following a baseline block with veridical visual feedback, a mixed trial block was introduced where, for the majority of trials, the visual feedback cursor was rotated 45° with respect to the position of the hand (Fig. 1A, rotation trials). Participants were cued on these trials to "move the cursor to the target", instructions shown previously to encourage strategic aiming (Vandevoorde and Orban de Xivry, 2019). Over the block, participants learned to compensate for the rotation on these trials, getting close (~40°) to the ideal 45° change in hand angle (Fig. 1B). We assume this performance reflects the combined effects of strategy use and implicit adaptation. To directly measure the latter, on randomly interleaved probe trials, participants were instructed to aim directly to the target and stop using any strategy employed on the rotation trials. To hone in on the state of implicit adaptation, no feedback was provided on these trials. We observed a marked difference in hand angles between rotation and probe trials, with the difference assumed to reflect the contribution of explicit aiming on rotation trials (Taylor *et al.*, 2014).

To wash out the effects of learning, participants completed an extended block of trials with veridical feedback. This was followed by a second learning block using the same design as initially experienced. Marked savings was observed on the rotation trials (Fig. 1C). We used a cluster-based permutation test to identify consecutive cycles that showed a significant difference between the two learning blocks, a method that does not rely on predefined windows to test savings (Maris and Oostenveld, 2007). This analysis revealed faster relearning over the first ~12 rotation cycles ($p<0.05$). On the implicit probe trials, the mean hand angle was numerically larger than in the first learning block for the early learning stage, but no significant clusters were found (Fig. 1D). Moreover, this effect did not persist, and, in fact, reversed by the end of the learning block ($p<0.05$). In addition, the aftereffect exhibited a robust attenuation from the first to the second learning sessions (all aftereffect cycles in fig. 1D, $p<0.05$).

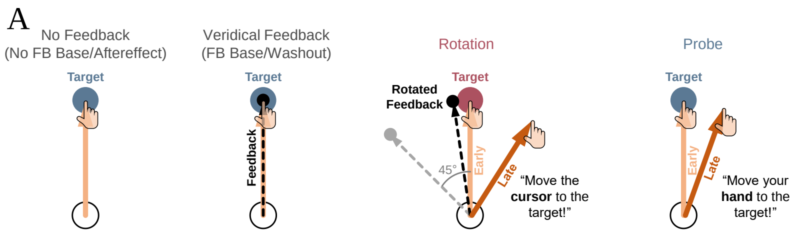
Consistent with prior work, Experiment 1 showed clear evidence of savings when participants used explicit strategies. Surprisingly, the results suggest that implicit learning may actually be attenuated during relearning. The one exception here was the initial probe cycles where we also saw slightly faster implicit learning. However, while these probe cycles may be evidence of (weak) savings, we worried that it might actually be a switching error (Rogers and Monsell, 1995), whereby participants fail to completely dispense their aiming when encountering the probe cue. While this cost would also be present in the first learning block, it would increase measured hand angles during probe trials of the second block, given the larger aiming strategy.

To address this concern, we conducted a second experiment in which we used task-irrelevant clamped feedback (Morehead *et al.*, 2017). Here, the strategic component is irrelevant since the participant is instructed to always aim directly to the target and ignore the feedback, which follows a fixed path away from the target (Fig. 2A). Importantly, this method measures implicit adaptation on every trial, so it is ideally suited to assess savings at all phases of learning, including at early stages. One group of participants (Test) experienced clamped feedback over two learning blocks, separated by a washout block (Fig. 2B). While these participants showed robust implicit adaptation in both learning blocks (Fig. 2C), the magnitude of adaptation was reduced on the second block, including during the early stages, and remained attenuated during an aftereffect block (Fig 2D).

To ensure that this attenuation of adaptation did not arise from fatigue, or habituation to a constant error, a control group was exposed to a single, extended block of clamped feedback (Fig. 2B). This group showed near-identical adaptation to the Test group over the cycles corresponding to the first learning block, but did not show any attenuation with continuous exposure to the clamp (Fig. 2C). The Control group's aftereffect (cycles 291-300) did not differ from that of the Test group after the first learning block (cycles 121-130) (Fig 2E), but was larger than the Test group's second aftereffect (cycles 291-300) (Fig. 2F, clusters in cycles 2-3 and 8-10 of aftereffect, $p<0.05$). The persistent degree of adaptation in this group argues against a fatigue or habituation account of the attenuation observed in the Test group.

We were initially surprised to observe attenuation of implicit learning in these experiments. This motivated us to take a fresh look at some past results of savings studies, both from our lab and from other labs. This review revealed a consistent pattern of attenuation of implicit adaptation upon relearning (see examples in Fig. 3). We believe this phenomenon was overlooked because it was secondary to the main goals of each study.

Taken together, relearning of visuomotor adaptation produces opposite effects on explicit and implicit processes that operate during sensorimotor adaptation: Savings is observed in the explicit system, presumably because this system can store and retrieve this explicit memory without it ever being forgotten. In contrast, implicit adaptation is attenuated during relearning.



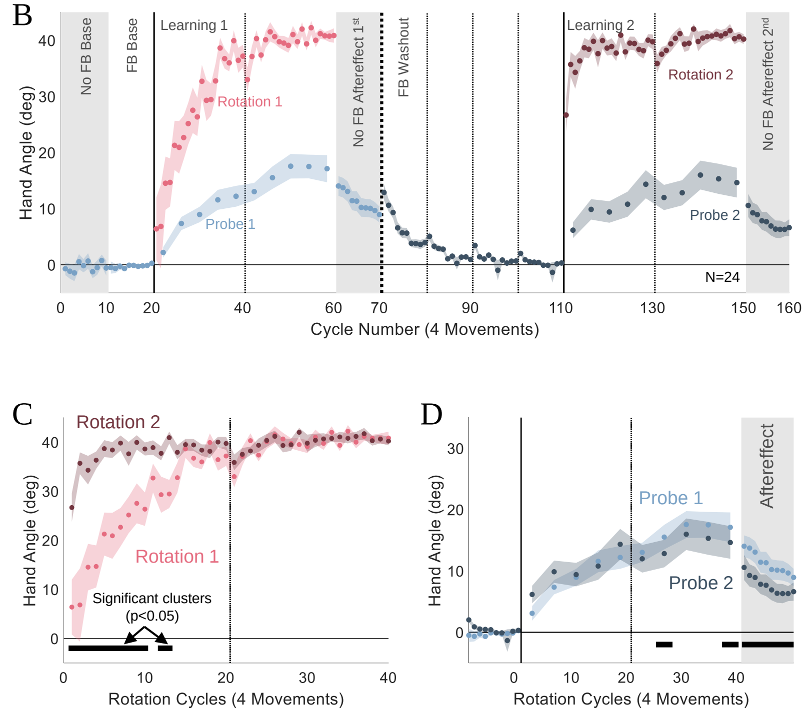
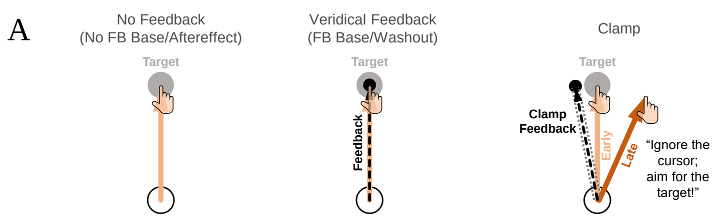


Figure 1. Experiment 1: Upon relearning a visuomotor rotation, explicit strategies show savings while implicit adaptation is attenuated. (A) Task-level schematics of all trial types. The participant was cued by the target color to aim for the target (blue) or to compensate for a rotated cursor (pink). (B) Time course of mean hand angle (N=24) during 1st (light colors) and 2nd (dark colors) learning sessions. (C, D) Mean hand angle time courses of the two sessions overlaying one another for the overall learning (explicit and implicit, C) and implicit (D). Horizontal thick black lines mark clusters of cycles that show significant difference between the blocks with p<0.05 probability. Cycle numbers in both C and D correspond to the cycles of the rotation trials. For all figures, dotted vertical lines denote one (thin) and two (thick) min breaks. Shaded margins represent standard error of the mean (SEM).



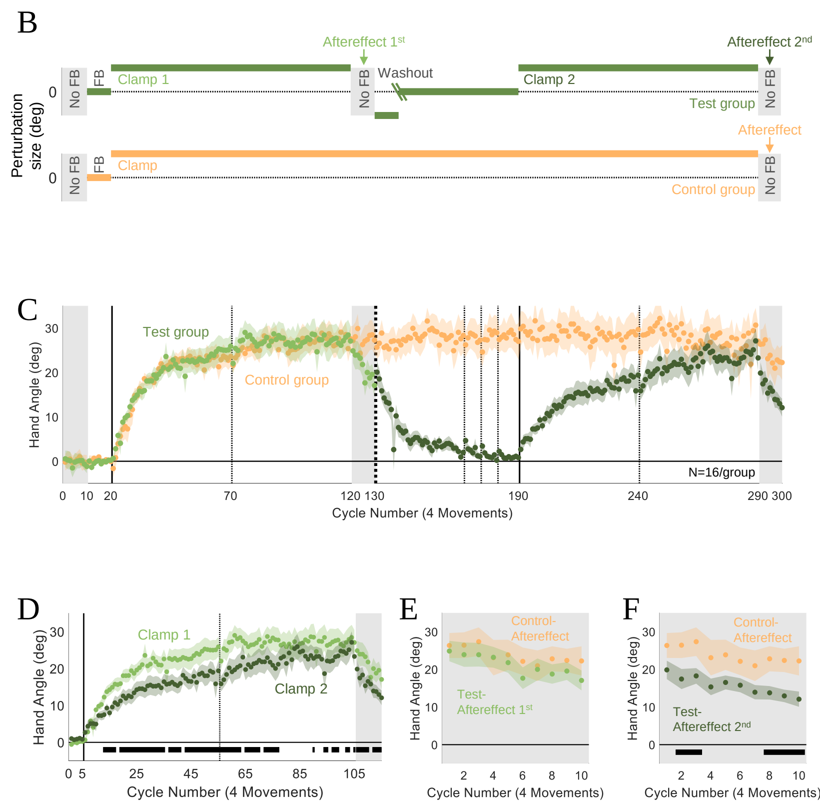


Figure 2. Experiment 2: Task-irrelevant clamped feedback revealed an overall attenuation of implicit adaptation upon relearning. (A) Task-level schematics of all trial types. On clamp trials, the visual feedback followed a fixed path rotated 15° from the target, and the participant was instructed to ignore it and keep aiming at the target. (B) Experimental protocol of two experimental groups: Test (green) and Control (orange). For the Test group, the green oblique lines in the Washout block represent a transition from a reversed-clamp phase to a veridical feedback phase, which occurred when the participant moved back to the target. (C) Time courses of mean hand angle for both groups (N=16/group). (D) Mean hand angle of the two sessions of the Test group overlaying one another, showing an attenuation of implicit adaptation upon relearning across multiple cycles throughout the learning and aftereffect blocks (horizontal thick black lines, p<0.05). (E, F) Mean hand angle time courses during the aftereffect block of the Control group overlaying the 1st (E) and 2nd (F) aftereffect blocks of the Test group, showing that the Control group did not exhibit any attenuation. Shaded margins represent SEM.

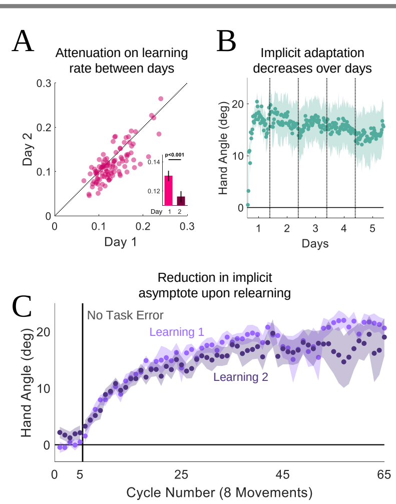


Figure 3. Prior evidence for attenuation upon relearning for implicit visuomotor adaptation. (A) Learning rate during adaptation to gradually changing visuomotor rotation over two days. Pink markers represent individual participants. Black diagonal dotted line represents the unity line. Bars and black vertical lines (inset) represent mean and SEM, respectively. (Stark-Inbar *et al.*, 2016). (B) Mean hand angle time course of implicit adaptation to visuomotor rotation over five days (separated by black vertical dotted lines). Implicit adaptation here was extracted by subtracting a reported aiming location from movement hand angle on every trial. Shaded margins represent the SEM. (Wilterson and Taylor, 2020). (C) Results from visuomotor rotation experiments, where a target jumps in a manner that eliminates task errors. With the remaining sensory prediction error (resulted from the rotated feedback), the change in behavior is considered implicit. The time courses of mean hand angle over two rotation blocks (originally separated by washout) overlaying one another. Light and dark purple signify learning blocks 1 and 2 of the experiment, respectively. Shaded margins represent the SEM. (Leow *et al.*, 2020).