

# How different cognitive strategies can influence implicit recalibration in visuomotor adaptation

Yiyu Wang<sup>1</sup> ([yw4722@princeton.edu](mailto:yw4722@princeton.edu))  
Jordan A. Taylor<sup>1,2</sup> ([jordanat@princeton.edu](mailto:jordanat@princeton.edu))

Department of Psychology<sup>1</sup>, Princeton Neuroscience Institute<sup>2</sup>, Princeton University, Princeton, NJ 08544

## Abstract

Visuomotor adaptation involves explicit strategies and implicit recalibration, but their interaction remains unclear. Strategies can take two forms: algorithmic strategies, involving mental simulation of motor solutions, and retrieval strategies, which rely on previously successful solutions. These strategies arise from distinct neural circuits, which are likely to influence cerebellar-dependent implicit recalibration in different ways. To explore this, we created conditions favoring algorithmic (visuomotor mental rotation) or retrieval strategies by varying training target set size, as retrieval is limited by working memory. We controlled for generalization and intertrial effects, isolating implicit recalibration. Preparation times confirmed distinct strategy adoption. While the magnitudes of implicit recalibration were similar, generalization breadth was narrower with retrieval strategies, suggesting stricter stimulus-response associations. Algorithmic strategies produced broader generalization. These findings confirm that algorithmic and retrieval strategies impact implicit recalibration differently, and demand that future efforts to characterize the pattern of implicit generalization must account for the unique contribution of different forms of explicit strategies.

**Keywords:** Sensorimotor Adaptation, Cognitive Strategy, Implicit Recalibration, Motor Generalization

## Introduction

Visuomotor adaptation is critical to the execution and maintenance of motor skills. In recent years, it has become clear that multiple processes contribute to performance improvements in visuomotor adaptation tasks, including, but not limited to, explicit aiming strategies and implicit recalibration (Krakauer et al., 2019; Morehead et al., 2015; Taylor et al., 2014). The operation of these process has been most successfully revealed by study of the visuomotor rotation task in which an angular mismatch is induced between movements of the hand and visual feedback (Cunningham, 1989; Krakauer et al., 2000). The visuomotor rotation task is ideal for the dissociation of explicit and implicit processes because the strategic solution is expressible in the same coordinates as the perturbation and implicit recalibration is expressed as an uncontrollable aftereffect (Taylor & Ivry, 2014).

While initial reports suggested that these processes operated with a considerable degree of independence, as they exhibit distinct learning signatures (Bond & Taylor, 2015; McDougale et al., 2015; Morehead et al., 2017) and likely arise from different neural systems (Areshenkoff et al., 2024; Butcher et al., 2017; Taylor & Ivry, 2014), more recent studies have suggested that strategies may directly or indirectly impact implicit recalibration (Albert et al., 2022; Day et al., 2016; McDougale et al., 2017). First, the focal point of implicit recalibration appears to be centered on the location

of an explicit aiming strategy, commonly referred to as plan-based generalization (Day et al., 2016; McDougale et al., 2017). Second, while explicit and implicit processes were thought to rely on distinct error signals – task-performance and sensory-prediction errors – it has recently been suggested that both processes make use of the same error signal, resulting in a competitive relationship (Albert et al., 2022). Finally, attempts to quantify their interaction with various methodologies has revealed a complex, nonlinear relationship (Maresch et al., 2021; t’Hart et al., 2024). As the differences in these studies make clear, the potential interaction between explicit strategies and implicit recalibration remains an open question.

One potential reason for these mixed findings is that subtle differences in task design may change the type of explicit strategy employed (McDougale & Taylor, 2019; Velazquez-Vargas & Taylor, 2024), which may ultimately impact implicit recalibration in different ways (Albert et al., 2022). At least two different types of strategies have been identified: an algorithmic strategy, which consists of mentally rotating an intended movement vector away from the target by an amount equal in magnitude and opposite to the direction of cursor rotation, and a retrieval strategy, which consists of caching a previously successful aiming solution in working memory. While this visuomotor mental-rotation strategy is highly flexible, it comes at a cost: preparation time linearly increases with the magnitude of the rotation, echoing classic Shepard mental rotation (Shepard & Metzler 1977). In contrast, following implementation of a successful strategy, on subsequent trials this strategy can simply be retrieved from working memory with little cost; however, this retrieval strategy is likely limited to previously experienced stimulus-response associations. Indeed, retrieval strategies do not generalize far beyond the exact conditions experience during training (McDougale & Taylor, 2019).

The complexity of the visuomotor rotation task appears to be a key determinant in which strategy is adopted. When the number of training targets (set size) is high, retrieval strategies prove to be ineffective as it exceeds working memory capacity (McDougale & Taylor, 2019; Velazquez-Vargas & Taylor, 2024). As a result, an algorithmic strategy must be adopted. Studies have found that the size aftereffect, considered to be a hallmark of implicit recalibration, varies with the number of targets (Bond & Taylor, 2015; Neville & Cressman, 2018). In addition, individuals with damage to the cerebellum appear to have considerably less impairment in visuomotor adaptation when there are only a few training targets (Gibo et al., 2013; Hadjiosif et al., 2024; Tsay et al.,

2022). It is possible that their rescued performance is the result of a retrieval strategy. Indeed, individuals with cerebellar damage appear to have a selective deficit with classic mental rotation and other algorithmic operations, but not conditions requiring scanning and retrieving from working memory (McDougle et al., 2022). As these different forms of strategy are likely supported by different neural subsystems of executive function and working memory (Luck & Vogel, 2013; Zacks, 2008), it is likely to assume that they link to the cerebellum in different ways (Bernard & Seidler, 2013; Buckner et al., 2011; Ravizza et al., 2006) and, ultimately, the operation of implicit recalibration.

In this study, we aimed to examine whether algorithmic and retrieval strategies differentially influence implicit recalibration. Two key factors could affect this assessment. First, plan-based generalization may introduce variability to the generalization function at adjacent targets, as a larger target set size is required to strengthen mental rotation. Second, an increase in intertrial interval (ITI) may lead to memory decay, reducing the magnitude of the aftereffect (Hadjiouisif et al., 2023). This increase in ITI could stem from both the additional time needed to revisit targets and the computational demands of mental rotation compared to the quicker retrieval of a smaller target set. Accounting for these factors, our design ensures that participants experience an equal number of intervening reaches with the same distribution. Additionally, to mitigate the effects of memory decay, we reinforced the memory of the reach prior to assessing the aftereffect at the same target location. We hypothesize that the type of strategy employed influences implicit recalibration, which would result in distinct generalization patterns. Specifically, an algorithmic strategy used in the visuomotor adaptation would result in a broader generalization breadth compared to retrieving a specific solution repetitively.

## Methods

### Participants

Participants were recruited through the subject pool maintained by the Department of Psychology at Princeton University. The study was approved by the Institutional Review Board, and all participants provided informed consent before participating in the experiment.

### Task design and procedure

Eighty-six participants (39 males, 47 females; mean age = 21 years, SD = 1.2 years) completed the experiment and were evenly divided into algorithmic-strategy and retrieval-strategy groups (see Fig. 2). They were tasked with attempting to bring a virtual cursor to a visually displayed target by dragging a stylus across the surface of a digitizing tablet (Wacom) in a center-out visuomotor reach adaptation task. Movements were sampled at a rate of 60 Hz and displayed on a 43.18 cm, 1024×768 resolution LCD Dell monitor running Windows 7. Visual feedback of hand

movements was occluded by the monitor, positioned 25 cm above the tablet (Fig.1).

On each trial, participants were guided to a central starting position (5 mm diameter), by a white ring that expanded or contracted based on the radial distance of their hand from the center. When the hand was 6 mm from the center, a white cursor (5 mm diameter) appeared, marking the hand's position as the start point. After holding the start position for 1 second, a target (10 mm diameter) appeared along a blue ring (80 mm diameter). Participants were instructed to make rapid “shooting” movements in an attempt to hit the target with the cursor. After leaving the start position, the cursor provided continuous, online visual feedback. When the hand passed the target, which was 80 mm away, a neutral “thunk” sounded to indicate completion of the reach. If the movement duration exceeded 0.3 seconds, an auditory warning (“too slow”) was triggered. Cursor feedback remained visible on the screen for 0.5 seconds before participants were guided back to the start location.

The experiment consisted of baseline, adaptation, and washout phases with a total of 484 trials. The baseline phase comprised three main phases: a 16-trial familiarization block period where general instructions were provided about performing the task, a 48-trial block where online feedback was withheld to measure any potential motor biases, and a final 16-trial period where online feedback was restored to ensure participants were calibrated to the task. Across all baseline phases, cursor feedback was veridical (Fig. 2A).

Following the baseline block, participants trained for 5 trials at a single target with a 45° visuomotor rotation before the main adaptation block began. The target location was pseudorandomly selected for each participant between 0:30:330° and was designated as the “critical” target location for evaluating the generalization function (see Fig. 2 E&H below). In addition, this practice period was designed to ensure they understood that the goal of the task was to counteract this rotation to get the cursor on the target. In addition, this allowed participants in the algorithmic group to pass through the discovery phase of strategy formation (Tsay et al., 2024) and participants in the retrieval group to begin to cache the aiming strategy (i.e., stimulus-response association), minimizing both the discovery phase and any effects of performing visuomotor mental rotation.

Following this brief rotation-practice period, the adaptation block began that consisted of reaching to 10 target locations in the workspace, which spanned from +/-60° to +/-180° centered on the critical target in 30° increments. Importantly, there were no training targets within 45° of the critical target – an important empty space for testing generalization (see Fig. 1C). For the algorithmic group, rotated cursor feedback was provided at these target locations. Having to counteract a rotation at numerous targets is a critical variable in pressuring participants to adopt a visuomotor mental rotation strategy (McDougle & Taylor, 2019) (Fig. 2E). In contrast, for the retrieval group cursor feedback was withheld at all target locations, except for the critical target (Fig. 2F). Choosing to have only a single target associated with a

rotation, should allow participants to cache the aiming solution (McDougle & Taylor, 2019). In addition, withholding feedback for all of these “dummy” targets to minimize any possible visuomotor mental rotation strategies and control for any potential intertrial time differences between the retrieval and algorithmic groups.

Within the adaptation block, participants periodically experienced a short set of Exclusion trials where cursor feedback was withheld, and participants were instructed to refrain from implementing any strategy (Maresch et al., 2021; t Hart et al., 2024; Taylor et al., 2014; Werner et al., 2015). For these Exclusion trials, the targets appeared between  $-45^\circ$  and  $45^\circ$ , in  $15^\circ$  increments, centered around the critical target to probe the generalization function of implicit recalibration. A total of 7 trials were included in each exclusion block, and the order of target locations was counterbalanced between blocks and across participants (e.g., Fig. 2G). Following these 7 Exclusion trials, cursor feedback was restored and participants practiced reaching all the other targets in the workspace. Prior to each set of Exclusion trials, participants made a single reach toward the critical target with rotated cursor feedback to ensure that implicit recalibration was maximal before assaying the generalization function of implicit recalibration. Just to summarize this complex “mini-block” structure during the adaptation block: participants made 40 reaches (except for block 1) to the other training targets (including the critical target), then one reach toward the critical target before reaching to 7 other targets neighboring targets, and then this mini-block would repeat.

A total of 356 trials were conducted, comprising all training and seven exclusion blocks (Fig. 2H). The critical target was presented on 40% of the trials and the sequence of target locations was randomized by controlling the intertrial intervals (ITIs), ensuring that the intervals for revisiting the critical target remained consistent across all participants. This design ensured sufficient training of the critical target while preventing the acquisition of stimulus-response associations in the algorithmic group and significant decay of implicit recalibration memory (Hadjiosif et al., 2023). In the end, the washout block was consisted of completing 48 trials of target reaching with no online feedback and no rotation.

The task was paused between all phases of the experiment, and text was displayed on the monitor that provided specific instructions for the upcoming trials (e.g., “During the following trials, the cursor will be removed and will not be rotated. You must stop using a strategy and reach to the target directly.”). In addition, feedback was withheld (on Dummy and Exclusion trials) to further remind the participants.



Figure 1. *Visuomotor adaptation setup*. A horizontally placed monitor occludes the participant’s hand from view, so that only the cursor on the screen provides visual information about hand position.

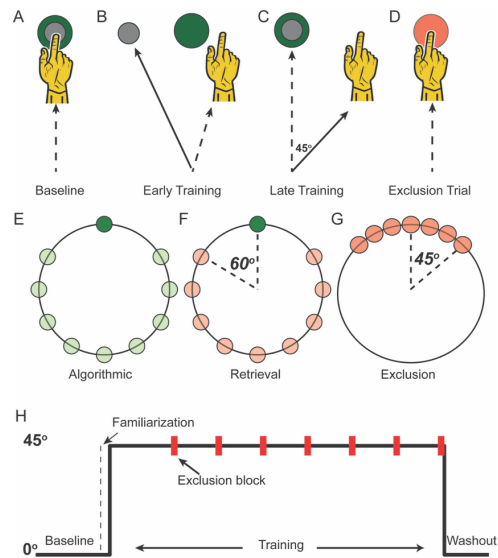


Figure 2. A) Baseline phase, in which the on-screen cursor veridically follows the participant’s hand movement; B) Early adaptation trial, showing a large directional error induced by the imposed rotation; C) Late adaptation trial, in which the participant has learned to counteract the rotation and thus produces a smaller error; D) Exclusion trial, where participants reach directly to the target without any cursor feedback or rotation; E) Target layout for the algorithmic group; F) Target layout for the retrieval group; G). Target layout used during the exclusion block; H) Schematic of the entire experimental procedure.

### Implicit Measures and Performance

Aftereffect, a hallmark of implicit recalibration, was assessed through Exclusion trials embedded within the adaptation session (see Fig. 2G&H). Each exclusion block was preceded by a top-up reaching trial to the critical target, minimizing adaptation loss due to memory decay (Hadjiosif et al., 2023). Seven targets, including the critical target, were randomized within each exclusion block and counterbalanced across adaptation sessions and participants. Participants were instructed to refrain from using any cognitive strategies and instead reach directly toward the target. During this process, online feedback and the rotation were removed. The hand angle at the moment of reach termination was calculated as a measure of implicit recalibration. In addition, this approach was employed to quantify the degree of adaptation for each trial throughout the task.

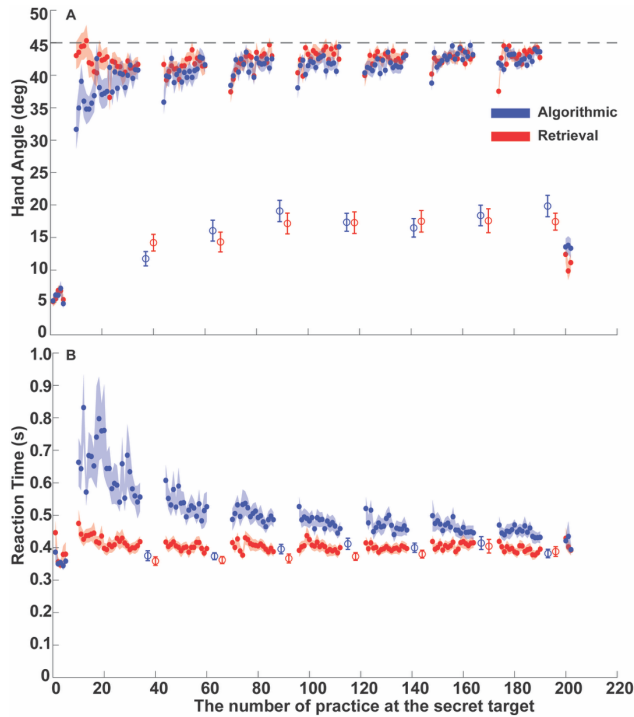


Figure 3. A) Trial-by-trial hand angle for the critical target; B) Trial-by-trial RT for the critical target. Shading represents SEM for the critical target during the Exclusion blocks.

## Analyses

**Performance:** There were two primary dependent measures used for analyses: endpoint hand angles and reaction time (RT). Endpoint hand angles were quantified as the distance between the final hand position at the completion of reach and the target location. Endpoint angles were used to measure performance during training and the degree and spatial extent of generalization of implicit recalibration. RT was defined as the time interval between the target onset and when the hand exceeded 5mm from the central starting location. RTs have been suggested to reflect computational processing demands, which have been shown to differ between the implementation of an algorithmic and retrieval strategy (McDougle & Taylor, 2019; Velazquez-Vargas & Taylor, 2024).

We performed a 2×2 mixed-design ANOVA to compare the means between the algorithmic and retrieval groups for early versus late phases of practice, as well as Exclusion blocks, across several measures, including the hand angle and reaction time (RT) of the critical target. Additionally, the mean RT of the critical between training and exclusion blocks was compared between the algorithmic and retrieval groups by *post hoc* test of the mixed design ANOVA, ensuring no algorithmic strategy was used in exclusion blocks.

The mean degree of adaptation prior to exclusion blocks was compared using repeated measures ANOVA to ensure that adaptation levels were consistent across groups. Additionally, the number of reaches and the final cursor positions within the ±45° aiming zone were quantified to

account for potential confounding factors influencing the results.

**Generalization:** hand angles for the 7 Exclusion trials were fit with Gaussian tuning functions (Brayanov et al., 2012; Poh & Taylor, 2019; H. Tanaka et al., 2009):

$$g(\theta) = k \cdot e^{-\frac{(\theta-\theta_0)^2}{2\sigma^2}} \quad (1)$$

The generalization function  $g(\theta)$  is centered on the target direction eliciting the greatest change in reach direction ( $\theta_0$ ), has an amplitude  $k$ , and is local with a width characterized by  $\sigma$ . Due to the limited sample size obtained from Exclusion trials, parameters of the Gaussian function were fit via bootstrapping the population (with exclusion and replacement) 1000 times. This method leverages the full distribution of samples (1000 total) and evaluates statistical significance based on the 95% confidence intervals from the bootstrap tails, with a significance level set at 0.05 (Fisher, 1993). Fits were optimized with the *fmincon* function in MATLAB.

RT was used as an indicator of the cognitive strategy applied during task performance. Consistent with prior research, the RT of the algorithmic group was expected to be significantly slower than that of the retrieval group.

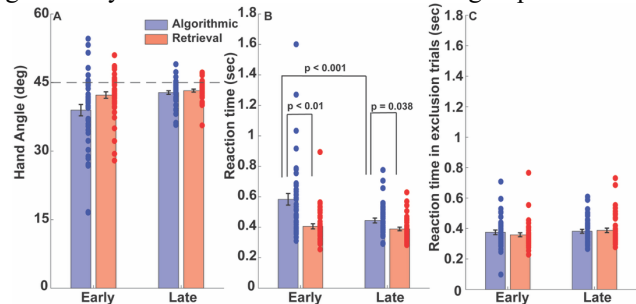


Figure 4. A) Averaged hand angle (early vs late); B) Averaged reaction time (early vs late); C) Averaged reaction time for exclusion blocks at the critical target (early vs late). Open circles are individual participants' data.

## Results

### Training

While the retrieval group appeared to counteract the 45° rotation more rapidly early in training, as expected given the task demands, the average hand angle for the target of primary interest – “critical” target – across all training blocks was slightly different between the groups ( $F(1,84) = 4.843, p = 0.031$ ; Fig. 3A, 4A). This difference was attributed to the variance in early practice between the groups ( $p = 0.023$ ), while similar performance was observed in late practice ( $p = 0.405$ ) (Fig. 4A). Importantly, there was a significant difference in RT between the groups ( $F(1,84) = 17.617, p < 0.001$ ; Fig. 3B, 4B). The algorithmic group displayed slower RTs (at the critical target) than the retrieval group, suggesting that they were employing a high-cost visuomotor mental rotation strategy. In contrast, the group, which was most likely implementing a cached strategy.

Exclusion trials, when cursor feedback is removed, and participants were instructed to refrain from implementing a strategy and were leveraged to measure the potential impact of the different kinds of strategies on implicit recalibration. In these trials, we find no group differences between groups at the critical target ( $F(1,84) = 0.088, p = 0.767$ ; Fig. 3B,4C). This indicates that all participants faithfully followed instructions to reach directly toward the target and not implement a strategy. Refraining from using a strategy during Exclusion trials was additionally supported by a significant difference in RT between the Training and Exclusion trials for the algorithmic group ( $p < 0.001$ ; Fig. 4B, C). RTs were similar between Training and Exclusion trials for the retrieval group, suggesting that caching a strategy may not incur much of a cost whatsoever ( $p = 0.121$ ; Fig. 4B, C).

### Generalization

A more interesting result emerges when inspecting the generalization function around the critical target on Exclusion trials (Fig. 5A). The generalization function is significantly broader for the algorithmic group (bootstrap,  $p < 0.01$ ). While this could be expected because the algorithmic group is required to implement the strategy over a larger region of space (at the other training targets), we were careful to exclude any training targets within  $90^\circ$  of the the critical target. However, even with this purposeful target arrangement of the workspace, it does not strictly preclude participants from reaching or aiming and receiving feedback in this zone. If participants aimed in this zone, then plan-based generalization could induce implicit recalibration here. A close inspection of the reach distributions does reveal a significant shift on one side of the critical target for the algorithmic group, which could account for this increase in generalization breadth (between  $-45^\circ$  and  $0^\circ$  in Fig. 5A). In contrast, on the other side the two distributions are approximately equivalent (shaded zone between  $0^\circ$  and  $45^\circ$  in Fig. 5A, with the tail of distribution being elongated for the retrieval group, yet their generalization is narrower. The narrower generalization observed in the retrieval group suggests more localized recalibration, likely constrained by the strict stimulus-response associations inherent to the retrieval strategy.

To ensure the reliability of these findings, a repeated measures ANOVA compared the degree of adaptation immediately before each exclusion block. Results showed no significant differences at the group level ( $p = 0.82$ ) or across training sessions ( $p = 0.06$ ). An independent t-test revealed no difference in final hand angles between groups ( $t(84) = 0.95, p = 0.35$ ) but the retrieval group had significantly more cursor appearances in the aiming zone than the algorithmic group ( $t(84) = -5.50, p < 0.01$ ), which could have resulted in more implicit recalibration. These results confirm that cursor appearances or final hand positions did not influence the generalization of implicit recalibration, suggesting that strategy use reshaped the generalization landscape, with algorithmic strategies, such as visuomotor mental rotation,

reflecting flexible movement planning and a retrieval strategy relying on stricter stimulus-response associations.

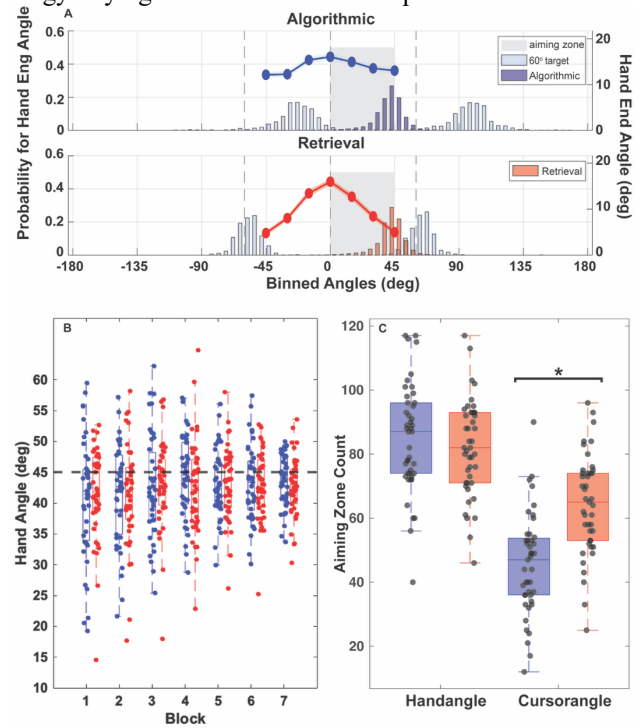


Figure 5. A) Generalization curves for algorithmic (blue) and retrieval (red) groups overlaid on histograms of final hand angles: dark bars show hand endpoint angle at the critical target, light bars show  $\pm 60^\circ$  targets; gray shading marks the aiming zone for the critical target. B) Mean adaptation magnitude immediately before execution. C) Number of trials in which final hand and cursor positions fell within the aiming zone.

### Discussion

The purpose of this study was to determine whether algorithmic and retrieval strategies have distinct effects on implicit recalibration during sensorimotor adaptation. We hypothesized that an algorithmic strategy would facilitate the encoding of flexible movement plans, resulting in a broader generalization breadth, whereas the retrieval strategy would produce a narrower generalization pattern due to its dependence on rigid stimulus-response associations. In part, this was based on a prior study where algorithmic strategies resulted in greater generalization than a retrieval strategy, although this study took efforts to prevent implicit recalibration, entirely leaving the possibility open (McDougle & Taylor, 2019). To ensure the reliability of our findings, the experimental design addressed potential confounding factors identified in previous studies, such as target set size (McDougle & Taylor, 2019; Velazquez-Vargas & Taylor, 2024), inter-trial intervals (ITIs; (Hadjiosif et al., 2023)), plan-based generalization (McDougle et al., 2017), memory decay (Hadjiosif et al., 2023), and unequal training durations per target. The degree of implicit recalibration and

generalization was assessed using Exclusion trials, where online feedback and the rotation were removed, and participants were instructed to refrain from using a strategy. While we found that both strategies produced similar levels of implicit recalibration at the critical target, the retrieval strategy led to a narrower generalization pattern compared to the algorithmic strategy.

### **Cognitive strategies**

In general, individuals can employ at least two distinct cognitive strategies to counteract visual perturbations. Algorithmic strategies, such as visuomotor mental rotation, enable the development of flexible, generalizable aiming solutions but require substantial computational effort (McDougle & Taylor, 2019). Conversely, memory retrieval offers a faster and computationally efficient approach for recalling known solutions but is limited in generalization and working memory capacity (McDougle & Taylor, 2019; Velazquez-Vargas & Taylor, 2024). Despite recent efforts to identify potential interactions of explicit strategies and implicit recalibration, the impact of different kinds of strategies on implicit recalibration has not been considered.

In the current study, we intentionally manipulated the target set size to enable participants in each group to effectively implement algorithmic and retrieval strategies. Importantly, we took several measures to control for other confounding variables. First, implicit recalibration and its generalization was centered on the critical target, with its locations matched in pairs across groups. Second, the algorithmic group was trained with a total of 10 targets, including the critical target, to pressure the application of visuomotor mental rotation. Third, nine “dummy” targets were introduced in the retrieval group to match the reach variability and intertrial time. Notably, this design effectively differentiated the strategy employed by each group, as evidenced by the elevated RTs observed in the algorithmic group (see Fig. 3B). Taken together, these efforts should ensure that the observed differences in implicit recalibration are not the result of subtle training exposure or statistical differences between conditions outside of the demands to implement an algorithmic or retrieval strategy.

### **Implicit recalibration and generalization**

Numerous studies have previously examined the interaction between the explicit and implicit processes. For instance, plan-based generalization provides direct evidence of how aiming strategies influence implicit recalibration, showing that the generalization pattern aligns with the explicit aiming direction (McDougle et al., 2017). As a result, the actual center of generalization likely corresponds to participants' aiming direction, which was not explicitly measured. It is possible that the retrieval strategy results in a greater degree of implicit recalibration at the aiming direction compared to algorithmic strategies. This could be explained by the fact that as training progresses with an algorithmic strategy, the aiming angle reduces while the proportional contribution of implicit learning to total adaptation increases

(McDougle et al., 2015; Taylor et al., 2014). This gradual shift likely brings the aiming direction closer to the target location, as supported by the observed decline in RTs within the algorithmic group (Fig. 2B), possibly reflecting smaller rotation angles over time. Conversely, the retrieval strategy relies on cached prior solutions, enabling the aiming direction to remain stable. This consistency in repetitive movements along the same direction may enhance implicit recalibration. Thus, each strategy could yield a distinct peak in the generalization pattern.

The frequencies of hand and cursor feedback in the aiming zone were quantified to rule out the possibility that the broader generalization breadth in the algorithmic group was due to a wider distribution of final hand and cursor presences within the aiming zone (Fig. 4C). This further supports the conclusion that the differences in the breadth of generalization patterns align with the strategies employed. On the process level, algorithmic strategies involve the computation of an intended movement angle that counteracts visual perturbation, requiring the transformation of the task demands into a flexible movement plan. This process is computationally demanding and allows for the derivation of generalizable solutions applicable to various spatial contexts (McDougle & Taylor, 2019). An algorithmic strategy necessitates processing errors relative to a global task framework, enabling broader learning transfer beyond the specific task context. At the neural level, an algorithmic strategy likely engages a broader population of neurons in the primary motor cortex (M1), enabling the generalizable encoding of motor plans (Pellizzer & Georgopoulos, 1993). In addition, the algorithmic strategy likely recruits an extensive and distributed network involving the prefrontal cortex, the posterior parietal cortex, and cerebellum, which collectively support the encoding of diverse movement patterns and enhance the expanded generalization. In contrast, a retrieval strategy ties learning to specific cached solutions, making it rigid and context specific.

Most generalization studies typically train participants at a single target location over many trials and probe generalization at other, untrained locations in the workspace. This logical design choice may have had the unintended consequence of only revealing generalization of implicit recalibration under the usage of a retrieval strategy (Bond & Taylor, 2015; Brayanov et al., 2012; McDougle et al., 2017). There have been only a few studies that have trained participants across the workspace, which requires modeling to extract the pattern of generalization (Donchin et al., 2003; Hirokazu Tanaka et al., 2009; Thoroughman & Shadmehr, 2000; Thoroughman & Taylor, 2005). As a result, the typically-reported narrow generalization function, and by extension, the neural tuning functions thought to underlie generalization (Brayanov et al., 2012; Donchin et al., 2003; Poh & Taylor, 2019; H. Tanaka et al., 2009; Taylor & Ivry, 2011) may not paint a comprehensive picture of the potential of implicit recalibration to generalize.

## Acknowledgments

We thank the members of the Intelligent Performance and Adaptation Laboratory (IPA Lab) in the Department of Psychology at Princeton University for their helpful discussions. The research reported in this manuscript was supported by grant R01NS131552 (awarded to JAT) from the National Institute of Neurological Disorders and Stroke (NINDS) of the National Institutes of Health (NIH). The funder played no role in study design, data collection and analysis, decision to publish, or preparation of the findings.

## References

- Albert, S. T., Jang, J., Modchalingam, S., Hart, B. M., Henriques, D., Lerner, G., Della-Maggiore, V., Haith, A. M., Krakauer, J. W., & Shadmehr, R. (2022). Competition between parallel sensorimotor learning systems. *Elife*, *11*. <https://doi.org/10.7554/eLife.65361>
- Areshenkoff, C. N., de Brouwer, A. J., Gale, D. J., Nashed, J. Y., Smallwood, J., Flanagan, J. R., & Gallivan, J. P. (2024). Distinct patterns of connectivity with the motor cortex reflect different components of sensorimotor learning. *PLoS Biol*, *22*(12), e3002934. <https://doi.org/10.1371/journal.pbio.3002934>
- Bernard, J. A., & Seidler, R. D. (2013). Relationships between regional cerebellar volume and sensorimotor and cognitive function in young and older adults. *Cerebellum*, *12*(5), 721-737. <https://doi.org/10.1007/s12311-013-0481-z>
- Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J Neurophysiol*, *113*(10), 3836-3849. <https://doi.org/10.1152/jn.00009.2015>
- Brayanov, J. B., Press, D. Z., & Smith, M. A. (2012). Motor memory is encoded as a gain-field combination of intrinsic and extrinsic action representations. *J Neurosci*, *32*(43), 14951-14965. <https://doi.org/10.1523/JNEUROSCI.1928-12.2012>
- Buckner, R. L., Krienen, F. M., Castellanos, A., Diaz, J. C., & Yeo, B. T. (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. *J Neurophysiol*, *106*(5), 2322-2345. <https://doi.org/10.1152/jn.00339.2011>
- Butcher, P. A., Ivry, R. B., Kuo, S. H., Rydz, D., Krakauer, J. W., & Taylor, J. A. (2017). The cerebellum does more than sensory prediction error-based learning in sensorimotor adaptation tasks. *J Neurophysiol*, *118*(3), 1622-1636. <https://doi.org/10.1152/jn.00451.2017>
- Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *J Exp Psychol Hum Percept Perform*, *15*(3), 493-506. <https://doi.org/10.1037//0096-1523.15.3.493>
- Day, K. A., Roemmich, R. T., Taylor, J. A., & Bastian, A. J. (2016). Visuomotor Learning Generalizes Around the Intended Movement. *eNeuro*, *3*(2). <https://doi.org/10.1523/ENEURO.0005-16.2016>
- Donchin, O., Francis, J. T., & Shadmehr, R. (2003). Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *Journal of Neuroscience*, *23*(27), 9032-9045.
- Gibo, T. L., Criscimagna-Hemminger, S. E., Okamura, A. M., & Bastian, A. J. (2013). Cerebellar motor learning: are environment dynamics more important than error size? *J Neurophysiol*, *110*(2), 322-333. <https://doi.org/10.1152/jn.00745.2012>
- Hadjiosif, A. M., Gibo, T. L., & Smith, M. A. (2024). The cerebellum acts as the analog to the medial temporal lobe for sensorimotor memory. *Proc Natl Acad Sci U S A*, *121*(42), e2411459121. <https://doi.org/10.1073/pnas.2411459121>
- Hadjiosif, A. M., Morehead, J. R., & Smith, M. A. (2023). A double dissociation between savings and long-term memory in motor learning. *PLoS Biol*, *21*(4), e3001799. <https://doi.org/10.1371/journal.pbio.3001799>
- Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor Learning. *Compr Physiol*, *9*(2), 613-663. <https://doi.org/10.1002/cphy.c170043>
- Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci*, *20*(23), 8916-8924. <https://doi.org/10.1523/JNEUROSCI.20-23-08916.2000>
- Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. *Trends Cogn Sci*, *17*(8), 391-400. <https://doi.org/10.1016/j.tics.2013.06.006>
- Maresch, J., Werner, S., & Donchin, O. (2021). Methods matter: Your measures of explicit and implicit processes in visuomotor adaptation affect your results. *Eur J Neurosci*, *53*(2), 504-518. <https://doi.org/10.1111/ejn.14945>
- McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *J Neurosci*, *35*(26), 9568-9579. <https://doi.org/10.1523/JNEUROSCI.5061-14.2015>
- McDougle, S. D., Bond, K. M., & Taylor, J. A. (2017). Implications of plan-based generalization in sensorimotor adaptation. *J Neurophysiol*, *118*(1), 383-393. <https://doi.org/10.1152/jn.00974.2016>
- McDougle, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor learning. *Nat Commun*, *10*(1), 40. <https://doi.org/10.1038/s41467-018-07941-0>
- McDougle, S. D., Tsay, J. S., Pitt, B., King, M., Saban, W., Taylor, J. A., & Ivry, R. B. (2022). Continuous manipulation of mental representations is compromised in cerebellar degeneration. *Brain*, *145*(12), 4246-4263. <https://doi.org/10.1093/brain/awac072>
- Morehead, J. R., Qasim, S. E., Crossley, M. J., & Ivry, R. (2015). Savings upon Re-Aiming in Visuomotor Adaptation. *J Neurosci*, *35*(42), 14386-14396. <https://doi.org/10.1523/JNEUROSCI.1046-15.2015>

- Morehead, J. R., Taylor, J. A., Parvin, D. E., & Ivry, R. B. (2017). Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *J Cogn Neurosci*, *29*(6), 1061-1074. [https://doi.org/10.1162/jocn\\_a\\_01108](https://doi.org/10.1162/jocn_a_01108)
- Neville, K. M., & Cressman, E. K. (2018). The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Exp Brain Res*, *236*(7), 2047-2059. <https://doi.org/10.1007/s00221-018-5282-7>
- Pellizzer, G., & Georgopoulos, A. P. (1993). Mental rotation of the intended direction of movement. *Current Directions in Psychological Science*, *2*(1), 12-17.
- Poh, E., & Taylor, J. A. (2019). Generalization via superposition: combined effects of mixed reference frame representations for explicit and implicit learning in a visuomotor adaptation task. *J Neurophysiol*, *121*(5), 1953-1966. <https://doi.org/10.1152/jn.00624.2018>
- Ravizza, S. M., McCormick, C. A., Schlerf, J. E., Justus, T., Ivry, R. B., & Fiez, J. A. (2006). Cerebellar damage produces selective deficits in verbal working memory. *Brain*, *129*(Pt 2), 306-320. <https://doi.org/10.1093/brain/awh685>
- Hart, B. M., Taqvi, U., Gastrock, R. Q., Ruttle, J. E., Modchalingam, S., & Henriques, D. Y. P. (2024). Measures of Implicit and Explicit Adaptation Do Not Linearly Add. *eNeuro*, *11*(8). <https://doi.org/10.1523/ENEURO.0021-23.2024>
- Tanaka, H., Sejnowski, T. J., & Krakauer, J. W. (2009). Adaptation to visuomotor rotation through interaction between posterior parietal and motor cortical areas. *Journal of neurophysiology*, *102*(5), 2921-2932.
- Tanaka, H., Sejnowski, T. J., & Krakauer, J. W. (2009). Adaptation to visuomotor rotation through interaction between posterior parietal and motor cortical areas. *J Neurophysiol*, *102*(5), 2921-2932. <https://doi.org/10.1152/jn.90834.2008>
- Taylor, J. A., & Ivry, R. B. (2011). Flexible cognitive strategies during motor learning. *PLoS Comput Biol*, *7*(3), e1001096. <https://doi.org/10.1371/journal.pcbi.1001096>
- Taylor, J. A., & Ivry, R. B. (2014). Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Prog Brain Res*, *210*, 217-253. <https://doi.org/10.1016/B978-0-444-63356-9.00009-1>
- Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci*, *34*(8), 3023-3032. <https://doi.org/10.1523/JNEUROSCI.3619-13.2014>
- Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, *407*(6805), 742-747.
- Thoroughman, K. A., & Taylor, J. A. (2005). Rapid reshaping of human motor generalization. *Journal of Neuroscience*, *25*(39), 8948-8953.
- Tsay, J. S., Kim, H. E., McDougle, S. D., Taylor, J. A., Haith, A., Avraham, G., Krakauer, J. W., Collins, A. G. E., & Ivry, R. B. (2024). Fundamental processes in sensorimotor learning: Reasoning, refinement, and retrieval. *Elife*, *13*. <https://doi.org/10.7554/eLife.91839>
- Tsay, J. S., Najafi, T., Schuck, L., Wang, T., & Ivry, R. B. (2022). Implicit sensorimotor adaptation is preserved in Parkinson's disease. *Brain Commun*, *4*(6), fcac303. <https://doi.org/10.1093/braincomms/fcac303>
- Velazquez-Vargas, C. A., & Taylor, J. A. (2024). Working memory constraints for visuomotor retrieval strategies. *J Neurophysiol*, *132*(2), 347-361. <https://doi.org/10.1152/jn.00122.2024>
- Werner, S., van Aken, B. C., Hulst, T., Frens, M. A., van der Geest, J. N., Struder, H. K., & Donchin, O. (2015). Awareness of sensorimotor adaptation to visual rotations of different size. *PLoS one*, *10*(4), e0123321. <https://doi.org/10.1371/journal.pone.0123321>
- Zacks, J. M. (2008). Neuroimaging studies of mental rotation: a meta-analysis and review. *J Cogn Neurosci*, *20*(1), 1-19. <https://doi.org/10.1162/jocn.2008.20013>