RESEARCH ARTICLE

Control of Movement

Working memory constraints for visuomotor retrieval strategies

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Abstract

Recent work has shown the fundamental role that cognitive strategies play in visuomotor adaptation. Although algorithmic strategies, such as mental rotation, are flexible and generalizable, they are computationally demanding. To avoid this computational cost, people can instead rely on memory retrieval of previously successful visuomotor solutions. However, such a strategy is likely subject to stimulus-response associations and rely heavily on working memory. In a series of five experiments, we sought to estimate the constraints in terms of capacity and precision of working memory retrieval for visuomotor adaptation. This was accomplished by leveraging different variations of visuomotor item-recognition and visuomotor rotation tasks where we associated unique rotations with specific targets in the workspace and manipulated the set size (i.e., number of rotation-target associations). Notably, from *experiment 1* to *4*, we found key signatures of working memory retrieval and not mental rotation. In particular, participants were less accurate and slower for larger set sizes and less recent items. Using a Bayesian latent-mixture model, we found that such decrease in performance was the result of increasing guessing behavior and less precise memories. In addition, we estimated that participants' working memory capacity was limited to two to five items, after which guessing increasingly dominated performance. Finally, in *experiment 5*, we showed how the constraints observed across *experiments 1* to *4* can be overcome when relying on long-term memory retrieval. Our results point to the opportunity of studying other sources of memories where visuomotor solutions can be stored (e.g., episodic memories) to achieve successful adaptation.

NEW & NOTEWORTHY We show that humans can adapt to feedback perturbations in different variations of the visuomotor rotation task by retrieving the successful solutions from working memory. In addition, using a Bayesian latent-mixture model, we reveal that guessing and low-precision memories are both responsible for the decrease in participants' performance as the number of solutions to memorize increases. These constraints can be overcome by relying on long-term memory retrieval resulting from extended practice with the visuomotor solutions.

Bayesian methods; explicit strategies; motor adaptation; working memory

INTRODUCTION

Adapting motor output in response to unexpected sensory feedback or changing environmental demands is an essential process for skillful motor execution (1–3). Although this process of sensorimotor adaptation was originally thought to be the result of a low-order, implicit process (4–7), in recent years it has become clear that higher-order cognitive strategies play a considerable role (8–10). In fact, implicit adaptation processes appear to be incapable of overcoming perturbations in a number of situations (11–14), and the use of cognitive strategies is necessary to improve performance (15). Despite the mounting evidence for the importance of

strategies in sensorimotor adaptation, we currently know very little about the underlying cognitive processes that support them.

In a prior study, we found evidence that people can use (at least) two broad classes of strategies in a visuomotor rotation task: an algorithmic strategy that involves the mental simulation of different aiming solutions to overcome the rotation and a retrieval strategy that can "cache" previously successful aiming solutions (16). Algorithmic strategies, operationalized as a form of mental rotation (17), can be flexible and generalizable (16, 18) but come at a computational cost. In particular, reaction times (RTs) linearly increase with the rotation magnitude (16, 19), indicative of the higher computational demands when

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the strategy is performed for longer—similar to the depth of tree search in planning. Indeed, people have a tendency to avoid situations that require greater mental rotation (20).

Alternatively, participants could forgo the computational cost of an algorithmic strategy by attempting to retrieve a previously successful aiming solution from a short-term memory cache (21, 22). In effect, participants could construct a stimulus-response look-up table between a target location and its corresponding aiming solution. Compared with algorithmic strategies, this greatly reduces the time it takes to implement the strategy and reduces movement variance around the solution (16). However, retrieval strategies are likely subject to capacity constraints of short-term memory: participants may be able to cache strategies when task complexity (set size) is low, but this approach may break down as complexity increases, based on studies of working memory capacity outside the motor domain (23–26).

Potential constraints of memory capacity for retrieval strategies could significantly limit their usefulness for visuomotor adaptation over the long term. Previous studies have shown that strategy implementation improves with training, in terms of speed and accuracy of execution (15, 16, 27). However, it remains an open question whether this is due to greater efficiency in the algorithmic computations for visuomotor mental rotation or whether it reflects a shift toward cached solutions being retrieved from memory (28). In classic Shepard-like mental rotation tasks, improvements in performance are thought to be the result of item-based memory retrieval for familiar stimuli rather than improvement in the algorithmic computations themselves (29–31). These findings are consistent with the instance theory of automatization of skills where early in learning tasks are performed using computationally demanding algorithmic processes but slowly give way to less demanding retrieval-based memory processes for familiar stimulus-response associations (28). Indeed, we have found that participants readily switch from an algorithmic strategy to a retrieval strategy over the course of training; however, this was only observed for conditions involving a few training targets in the workspace, suggesting that memory capacity limitations may constrain strategy selection and, ultimately, their efficacy for visuomotor adaptation (16).

Here, in a series of studies, we sought to determine if retrieval strategies for visuomotor adaptation are subject to constraints of working memory, in terms of capacity and precision. Although previous studies have addressed memory retrieval processes in visuomotor tasks (17), and more recently in visuomotor rotation experiments (16), they have remained agnostic to situations where visuomotor solutions are experienced a single, or few, time(s). Such scenarios are a key component of human experience and have been shown to guide decision-making in a wide variety of settings (32–35).

To address this question, we made use of the visuomotor rotation task, which has not only served as a model paradigm for studying adaptation (36, 37) but is also ideally suited to study cognitive strategies since the solution is expressible in the relevant dimension of the task (38). We combine this adaptation task with classic experimental approaches, such as item-recognition (17, 39), probed recall (40), and computational

models, to study visuospatial working memory (41–43). Through this set of experiments, we find that retrieval strategies are constrained to a range of two to five items, consistent with the findings of visuospatial working memory but can be overcome via long-term memory following substantial repetition. These findings suggest that retrieval strategies may be useful for visuomotor adaptation over the long term.

MATERIALS AND METHODS

Participants

Seventy-three right-handed undergraduate students (34 male, 37 female, 1 nonbinary, and 1 preferred not to say; mean age = 20, SD = 1.2) from Princeton University were recruited through the psychology subject pool. Sample sizes were based on previous studies on visuomotor adaptation where the number of subjects per condition typically ranges from 10 to 20 participants per condition. A post hoc power analysis with a desired statistical power of 85% revealed that the estimated sample size for our experiments would be 15 participants for *experiment 1*, 7 participants for *experiment 2*, 12 participants for *experiment 3*, and 12 participants for *experiment 4*. The experiments were approved by the institutional review board (IRB), and all participants provided written informed consent before performing the experiment.

Apparatus and Task Design

Participants performed horizontal, center-out movements holding a digital pen over a Wacom tablet. The movements were recorded at a sampling rate of 60 Hz in a 43.18-cm, $1,024 \times 768$, LCD Dell monitor running on Windows 7. Visual feedback of the hand was occluded by the monitor, which was mounted 25 cm above the tablet. On every trial, the participants attempted to find the monitor's center ($d = 5$ mm). They were aided by a white ring that either expanded or contracted with the radial distance of the participant's hand from the center. When the hand was 6 mm from the center, a red circular cursor ($d = 4$ mm) appeared at the current hand position—the start position. After holding the start position for 1 s, a circular target ($d = 7$ mm) appeared along a blue ring ($d = 70$ mm). The participants were instructed to make ballistic center-out movements as fast and accurately as possible (16, 17) such as to slice through the blue ring, with the ultimate goal of hitting the target with the cursor. To achieve the latter, each experiment had varying requirements that will be described later. After leaving the start position, visual feedback of the cursor was removed. If the movement duration between leaving the start position and crossing the blue ring exceeded 0.6 s, the participants received an auditory warning ("too slow"). When the participants' hand exceeded the blue ring radius, the cursor would show up along the ring. If it appeared on top of the target—a hit—the participants would hear a pleasant sound ("ding"); otherwise, they would hear an unpleasant sound ("buzz")—a miss. The cursor feedback was delayed 0.5 s to reduce the possible role of implicit adaptation (44) in the experiments. The cursor end point feedback remained on the screen for 0.5 s, after which participants would attempt to find the center to begin the next trial. Every experiment consisted of a series of blocks

separated by a pause, where the message "Wait for experimenter's instructions" would appear and participants would be told what to do in the next block. All experiments were adapted such that they did not exceed 1 h.

Experiment 1: Visuomotor Item-Recognition

In this experiment ($n = 15$), we sought to establish that participants could use a retrieval strategy to solve a visuomotor rotation without using a visuomotor mental rotation strategy. Here, we embedded a visuomotor rotation task in the context of a "classic" working-memory item-recognition task (17, 45). The experiment unfolded over a series of encoding and retrieval phases. In the encoding phase, the participants first observed a sequence of white targets displayed one at a time along the blue ring and were asked to memorize them (Fig. 1A). Each target remained on the screen for 0.8 s and was separated from the next one by 0.15 s. The stimuli presentation and the time interval between them was the same as in the study by Pellizzer and Georgopoulos (17). In addition, Oberauer et al. (25) presented an ample collection of findings in working-memory research pointing out that there are no further improvements in accuracy for presentation durations beyond 50–100 ms. The angular location of the targets over the ring was randomly sampled without replacement out of 24 possible locations ranging from 0° to 345° in steps of 15°. After 0.2 s of the sequence presentation, the retrieval phase began. In this phase, one target was selected randomly from the sequence and displayed in green to the participants ("cued" target). The participants were instructed to perform a reaching movement to the location of the target that appeared immediately after it in the sequence ("subsequent" target). We manipulated two independent variables: the sequence length, which ranged from two to five targets, and the angular separation between the cued and subsequent target, which ranged from −90° to 90° in steps of 15° and excluding 0°, giving a total of 12 values. Importantly, the cursor end point position was rotated in the opposite direction and with the same magnitude as the angular separation between the cued and subsequent target (Fig. 1A). Therefore, if the participants correctly reached the

position of the subsequent target, they would hit the cued target with the cursor—in effect, a visuomotor rotation task. A crucial prediction from this experiment was that if participants were performing memory retrieval, their RTs would increase with the sequence length, indicative of memory scanning (45), but not with the rotation magnitude, indicative of mental rotation (16).

To make sure the participants understood the experiment, they underwent a series of preparation blocks where they first learned to find the center of the tablet and make straight reaching movements to the targets (48 trials: 24 trials with feedback and 24 trials without feedback); then, they were exposed to target sequences with all lengths and rotation magnitudes to get familiarity with the task (48 trials). Then, in the actual experiment, each sequence length and rotation magnitude combination was tested three times (144 trials). At the end, participants underwent a washout block (24 trials) where they were instructed to reach directly to targets while not receiving end point feedback. The experiment had a total of 264 trials.

Experiment 2: Extended Visuomotor Item-Recognition

Since guessing behavior in *experiment 1* consistently remained below 50% across all sequence lengths, we hypothesized that participants' working-memory capacity exceeded the demands imposed by the task. Therefore, in *experiment 2* ($n = 13$), we extended the design of *experiment 1* to include sequences up to length 10. We were particularly interested in whether the guessing behavior and memory precision would continue to increase and decrease, respectively, and the point where they would level off, if at all. Considering that in *experiment 1*, RTs did not change with the rotation magnitude—suggesting no mental rotation—we relaxed the control of this variable for *experiment 2*. We only made sure that all rotation magnitudes tested in *experiment 1* were repeated at least three times across the experiment and that they added up to 0 to prevent a bias for one side of the rotation. Each sequence length from 2 to 10 was tested 15 times. In total, there were 252 trials divided into learning to find the center and make reaching movements (48 trials: 24 trials with feedback and 24 trials
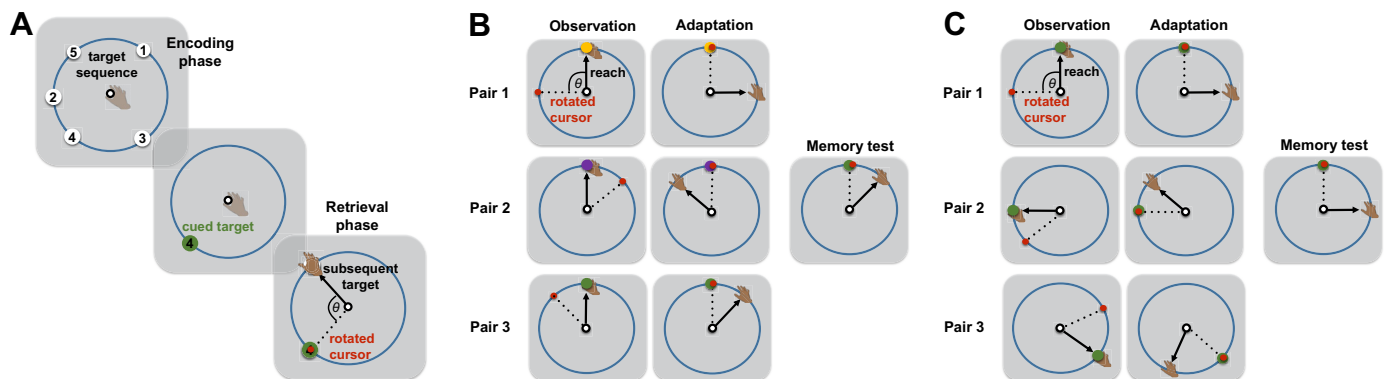

Figure 1. *A*: visuomotor item-recognition task from *experiments 1* and *2*. A sequence of targets appeared, one at a time, on a circle followed by the presentation of one target from that sequence. The participants had to reach the location of the subsequent target on the sequence. *B*: visuomotor rotation recall task from *experiment 3*. A sequence of pairs of trials was shown. In the first trial of each pair, the participants reached to the colored target and observed the rotation associated with it (observation). In the next trial, they attempted to counteract the rotation (adaptation). In the memory test, one colored target from the ones in the sequence was shown (target of *pair 3* is shown as an example) and participants had to counteract the rotation associated with it. *C*: visuomotor rotation recall from *experiment 4*. In this experiment each rotation value was associated with a different target location instead of colors as in *experiment 3*. Target of *pair 1* is shown as an example of the memory test.

without feedback), practice with the target sequences (45 trials; each length tested three times), experiment (135 trials), and washout (24 trials). Apart from these specifications, everything else remained as in *experiment 1*.

Experiment 3: Visuomotor Rotation Recall (Color)

Admittedly, the sequential design of *experiments 1* and *2* departs from what is typically required in a visuomotor rotation task. Therefore, in *experiment 3* ($n = 15$), we adopted a more conventional trial-pair design (16) to test the working-memory constraints of retrieval strategies. In this design, the participants were first exposed to an observation trial followed by an adaptation trial. On the observation trial, participants were instructed to reach directly to a presented target and to observe the cursor rotation. On the adaptation trial, they were tasked with counteracting the rotation (Fig. 1*B*). These trial-pairs were presented in sequences ranging from one to five (5 targets was the estimated capacity above which guessing began to dominate performance in *experiment 2*). After the sequence presentation, there was a memory test in which a target from the sequence was selected and participants had to retrieve the aiming solution for that target to successfully counteract the rotation. In order for participants to easily recognize which type of trial they were in, a text near the center would indicate "Observation," "Adaptation," or "Memory test" in the corresponding trial.

The target location was fixed at 90° for all trials, and target colors were used to indicate the different rotation magnitudes. We chose color to differentiate between rotation magnitudes, as it is a feature that has been widely investigated in studies of working memory (46). For every new sequence, the target colors were randomly sampled without replacement out of five possible options: black (rgb = [0,0,0]), orange (rgb = [255,53,51]), green (rgb = [0,255,0]), yellow (rgb = [255,255,0]), and purple (rgb = [178,102,255]). Similarly, the rotation magnitudes associated with each target color were randomly sampled without replacement out of five possible magnitudes: 30°, 45°, 60°, 75°, and 90°, with randomized signs. The random selection of the target colors and their associated rotation values rendered the learning from the previous trials irrelevant for the current trial. Therefore, performance depended solely on a single learning episode. Importantly, although participants could experience five possible rotation magnitudes during the sequence of pairs, only three were evaluated in the memory test: ±30, ±60, and ±90. The reason for this was to maintain the duration of the experiment similar to *experiment 1* and *2* while keeping the experiment counterbalanced. Based on previous studies (16), we believed that any effect of the rotation magnitude on performance, e.g., RTs increasing due to mental rotation, would show up with the tested magnitudes. There were a total of 446 trials divided into learning to find the center and making reaching movements (24 trials: 8 trials with feedback and 16 trials without feedback), practice with the trial-pair design (16 trials), practice with the sequence of pairs (15 trials), the experiment (375 trials), and washout (16 trials).

Experiment 4: Visuomotor Rotation Recall (Location)

To provide further evidence of the capacity limitations of retrieval strategies in standard visuomotor rotation paradigms,

in *experiment 4* ($n = 15$), we varied the design of *experiment 3* such that instead of colors, each rotation magnitude was associated with a different target location. For every new sequence, the target locations of each pair were randomly sampled without replacement out of eight possible values ranging from 0° to 315° in steps of 45°. Here, the target color was green throughout the experiment. Similar to *experiment 3*, the random selection of the target locations and their associated rotation values aimed to prevent the learning from the previous trials affect the performance in the current trial. This variation would more closely resemble previous studies of dual adaptation (47) and pair-trial design (16). Apart from these changes, everything else remained as in *experiment 3*, having a total of 446 trials.

Experiment 5: Visuomotor Rotation Recall (Long-Term Retrieval)

In this final experiment ($n = 15$), we aimed to study whether the limited working-memory capacity shown particularly in *experiment 4* (around 2 elements) would be ameliorated as memories consolidate into long-term storage. In particular, we exposed participants to only sequences of length 5 and where the target locations were distinct for each rotation magnitude as in *experiment 4*. Unlike *experiment 4*, this time the rotation magnitude associated with a given target location remained the same across the experiment; however, its position within the sequence was randomized at every new sequence such that participants did not learn a particular arrangement of the trial-pairs. We expected that, over trials, participants would learn the target-rotation associations and guessing behavior would progressively decrease, whereas memory precision would increase. There were a total of 463 trials, which consisted of learning to find the center and making reaching movements (24 trials: 24 trials: 8 trials with feedback and 16 trials without feedback), practice with the trial-pair design (16 trials), practice with the sequence of pairs (22 trials), the experiment (385 trials: 35 sequences), and washout (16 trials). Apart from the aforementioned changes, everything else remained as in *experiment 4*.

Behavioral Data Analysis

All analyses were performed using the R statistical software version 3.2.2 (48) or MATLAB version 2022a (49). The core dependent variables in our experiments were reaction times (RTs), target errors, unsigned errors, and adapted magnitudes. RTs were defined as the time interval between the target presentation and participants' departure from the start position. Target errors were defined as the angular distance (in degrees) between the cursor and the target position. Unsigned errors refer to the absolute value of the target errors. Adapted magnitudes refer to the absolute angular distance of the hand with respect to the target. All behavioral measures were computed at the subject level, except for the target error distributions, where we pooled the data across participants. Linear regression models and correlation coefficients were performed using the *lm* and *cor* functions on R, respectively. For correlations, we provide both the Pearson and Spearman coefficients. Data points were excluded from analysis if they corresponded to false alarms. A false alarm refers to a trial where participants moved before the target was presented.

Guessing and Memory Precision Analysis

To disentangle the cognitive processes that gave rise to participants' performance in our tasks, we adopted a Bayesian latent-mixture approach (43, 50, 51). In particular, we assumed that errors in the tasks could be generated by participants sampling from two sources: a memory distribution, represented by a Von Mises distribution, and a guessing distribution, represented by a uniform distribution—a common approach in studies of spatial working memory (41). Given that, with the exception of *experiment 1,* the number of data points per subject for each sequence length ranged between 3 and 15, we opted to infer the mixture model parameters in all experiments at the group level to obtain more reliable estimates. The graphical representation of the mixture model for all experiments is shown in Fig. 3C. Here, nodes represent the variables in our model and arrows represent how they influence each other. Shaded nodes are observed variables, whereas unshaded nodes are unknown variables. Circular nodes indicate continuous variables, whereas squared nodes indicate discrete variables. The plates represent independent replications of the graph structure. On the right side of the graph in Fig. 3C, we show the model specifications, including prior distributions.

In practice, we implemented the model using the following procedure: for every sequence length, the densities from a Von Mises distribution and a uniform distribution were obtained for every target error. For numerical stability, we used the logarithm of the densities. An indicator random variable z for every error and sequence length selected which of the two distributions was assumed to have generated the target error using their (log) densities and the "ones trick"

described in the study by Lee and Wagenmakers (43). Briefly, the "ones trick" allows us to reliably sample from a target distribution—in our case, the mixture distribution—using simpler distributions, given that our target distribution is not available in the inference library.

The indicator random variable z was sampled from a Bernoulli distribution with parameter ϕ for every sequence length. This parameter represents the proportion of errors believed to be generated by a uniform distribution, i.e., the guessing rate. The Von Mises distribution has a mean parameter, μ, and a concentration parameter, κ, for each sequence length. The latter reflects the dispersion in the distribution and in our context represents the memory precision. To study serial position effects in our experiments, we varied the structure of this model such that the parameters were estimated per position in the sequence (instead of per sequence length).

In addition to the latent mixture model, we also perform inference on a model that assumes no guessing, i.e., a simple Von Mises distribution. We compared the predictive accuracy of the models using leave-one-out cross-validation implemented in R code based on the study by Vehtari et al. (52, 53).

The posterior distribution of the model parameters was approximated using the software package JAGS (54) implemented in R code. We used three independent chains with 1.2×10^5 samples each. A burn-in period (initial samples that were discarded) of 2×10^3 samples and a thinning of 2 (one every two samples was selected) were used to encourage convergence and reduce autocorrelation between samples. This gave a total of 1.5×10^4 posterior samples for each group parameter. The additional JAGS module jags-vonmises (available on
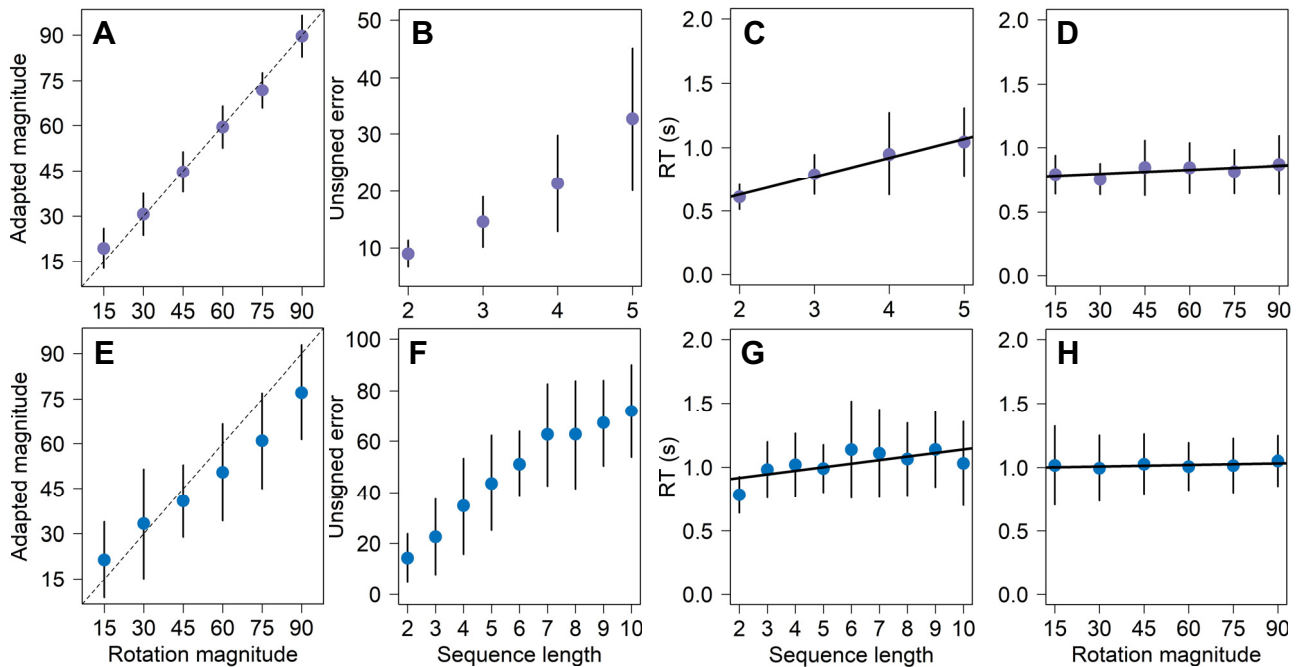

Figure 2. Behavioral results of *experiment 1* (purple) and *experiment 2* (blue). *A* and *E*: per-subject mean of adapted magnitude for each rotation magnitude. The dashed lines indicate performance when perfectly counteracting the rotation. *B* and *F*: per-subject mean of unsigned errors for each sequence length. *C* and *G*: per-subject median of reaction times for each sequence length. *D* and *H*: per-subject median of reaction times for each rotation magnitude. Black solid lines on reaction times (RTs) plots show the linear models fitted to the data. Error bars represent the standard deviation with respect to the mean.

https://github.com/yeagle/jags-vonmises) was used to compute Von Mises (log) density values. Convergence of the chains was assessed using the standard potential scale reduction statistic $\hat{R}$ (55). Values of $\hat{R} < 1.1$ generally indicate that the chains have converged. All the $\hat{R}$ values in our models were below this threshold.

Given that parameter inference was implemented at the group level, and due to the large number of posterior samples, we performed the statistical analyses in the modeling sections using a subsampling procedure (56). In particular, we drew 1,000 samples of size b without replacement from the posterior samples of the group parameters, where b was equal to the number of participants for the corresponding experiment. We computed the statistic of interest for each of the 1,000 samples and generated a distribution of its value given all samples. We report the 95% confidence interval (CI) based on this distribution. For example, in *experiment 1*, to test whether there was a correlation between the guessing rate θ and the sequence length, we sampled 15 values of θ without replacement from the posterior distribution of each sequence length (2–5 targets), giving a total of 60 data points, over which we performed the correlation test. We performed this step 1,000 times and reported the 95% CI of the correlation coefficient based on the resulting distribution.

RESULTS

Experiment 1

Behavioral results.
The goal of our first experiment was to verify that people can leverage retrieval strategies, instead of an algorithmic strategy (i.e., mental rotation), to successfully solve a visuomotor rotation task and to estimate the precision of retrieval strategies. To test this, participants ($n = 15$) performed a visuomotor item-recognition task (17, 45), where they first observed a sequence of targets, ranging from two to five targets (set size), that were displayed one at a time along a ring (Fig. 1A; see MATERIALS AND METHODS for details). Then, a cued target from the sequence was presented, and the goal was to reach to the location of the subsequent target in the sequence. Within the item-recognition task, we embedded a visuomotor rotation task by manipulating the angular rotation between the end point cursor feedback and the end of the reach. Importantly, the angular difference between the cued and subsequent target were varied to simulate a visuomotor rotation, which ranged from −90° to 90°. This way, if participants correctly reached to the subsequent target in the sequence, they would also hit the cued target with the cursor. We hypothesized that if participants were using retrieval-based strategies, then RTs to the subsequent targets would not vary with the angular difference between the cued and subsequent targets (i.e., visuomotor rotation magnitude). After a given sequence was experienced, the relationship between the target locations and rotations was randomized for the next sequence.

Overall, participants successfully reached the subsequent target across the different rotation magnitudes, as reflected in a significant positive correlation between the adapted magnitude and the rotation magnitude [$r^{\text{Pearson}}(178) = 0.96$, $P < 0.001$; $r^{\text{Spearman}}(178) = 0.96$, $P < 0.001$; Fig. 2A].

However, accuracy decreased with the sequence length, as suggested by larger unsigned errors for longer sequences [$r^{\text{Pearson}}(58) = 0.74$, $P < 0.001$; $r^{\text{Pearson}}(58) = 0.79$, $P < 0.001$; Fig. 2B], providing preliminary evidence that the precision of retrieval-based strategies is subject to set size constraints.

A key prediction of this study was that RTs would increase with the sequence length (17) but not the rotation magnitude (16) if the participants were performing memory retrieval instead of mental rotation. Indeed, we found that sequence length [$\beta = 0.14$, $P < 0.001$, $R^2 = 0.35$, $F(1,58) = 32.18$; Fig. 2C], but not rotation magnitude [$\beta = 0.001$, $P = 0.15$, $R^2 = 0.02$, $F(1,88) = 2.02$; Fig. 2D], significantly predicted the median of participants' RTs in a linear regression analysis. In addition, a linear regression analysis performed at the individual level over RTs also revealed that the coefficient for sequence length was significantly greater than zero [$t(14) = 6.17$, $P < 0.001$; Supplemental Fig. S1A].

As a key property of working memory retrieval, we looked for serial position effects on performance and found that unsigned errors were indeed smaller [$r^{\text{Pearson}}(58) = -0.57$, $P < 0.001$; $r^{\text{Spearman}}(58) = -0.55$, $P < 0.001$; Supplemental Fig. S2A] and RTs lower [$r^{\text{Pearson}}(58) = -0.40$, $P = 0.001$; $r^{\text{Spearman}}(58) = -0.50$, $P < 0.001$; Supplemental Fig. S2E] for more recent targets in the sequence (i.e., a recency effect).

Modeling results.
Following previous work on spatial working memory (41, 42), we analyzed the target error distributions in our task (Fig. 3A) using a Bayesian latent-mixture model to better characterize the precision of retrieval strategies (43, 50, 51; Fig. 3C). In particular, we assumed that target errors were generated by either a memory distribution, represented by a Von Mises distribution, or a guessing distribution, represented by a uniform distribution. The Von Mises distribution is similar to a normal distribution but adapted to circular data given the structure of our reaching tasks. We implemented this model at the group level to have enough data points to generate reliable estimates of the distribution of the parameters. For our analyses, we focused on the group guessing rate parameter (θ) and the group memory precision parameter (κ) of the distribution (see MATERIALS AND METHODS for details).

As expected from previous studies (42), we found that the guessing rate increased with the sequence length ($r^{\text{Pearson}} = 0.98$, 95% CI [0.97, 0.98]; $r^{\text{Spearman}} = 0.96$, 95% CI [0.96, 0.96]; Fig. 3D), whereas the precision of the memory distribution decreased ($r^{\text{Pearson}} = -0.89$, 95% CI [−0.86, −0.92]; $r^{\text{Spearman}} = -0.89$, 95% CI [−0.86, −0.92]; Fig. 3E). These modeling results are consistent with the decrease in accuracy observed in participants' unsigned errors (Fig. 2B) and the pooled target error distributions (Fig. 3A). Furthermore, we were interested in whether the guessing rate and the precision of the memory distribution would vary depending on the position of the target in the sequence (i.e., serial position effects). Indeed we found a negative correlation between the target position in the sequence and the guessing rate θ ($r^{\text{Pearson}} = -0.95$, 95% CI [−0.94, −0.97]; $r^{\text{Spearman}} = -0.94$, 95% CI [−0.92, −0.96]; Fig. 3F), indicating that across sequence lengths, participants guessed less for more recent targets. Furthermore, we found a positive correlation between the memory precision κ and the position of the
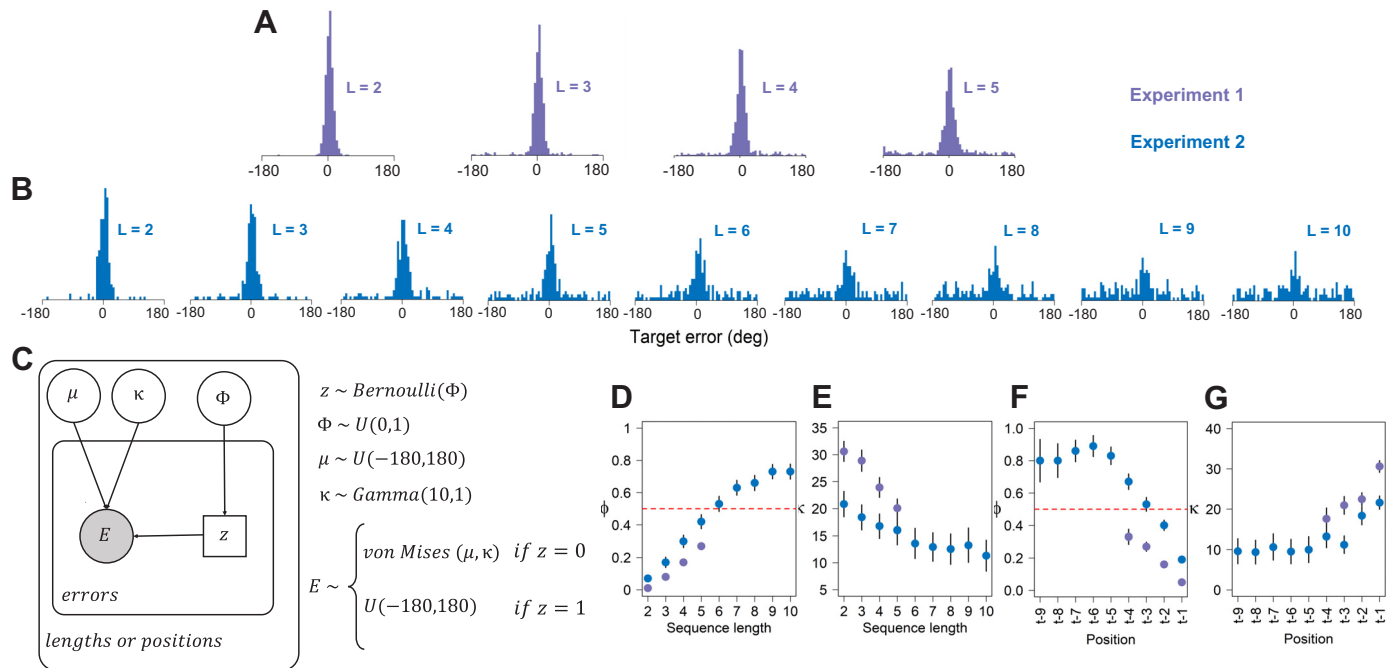
Figure 3. Analysis of target error distribution using a Bayesian latent-mixture model. *A* and *B*: pooled target error distributions for each sequence length of *experiment 1* and *experiment 2*. *C*: graphical representation of the Bayesian latent-mixture model of target errors (see MATERIALS AND METHODS for details). *D*: posterior distribution of the group guessing rate parameter, ϕ, for each sequence length. The red dashed line indicates $\phi = 0.5$. *E*: posterior distribution of the group memory precision parameter, κ, for each sequence length. *F*: posterior distribution of the group guessing rate parameter, ϕ, for the last ($t - 1$), second to last ($t - 2$), and so on, targets across sequence lengths. *G*: same as (*F*) but for the group memory precision parameter, κ. Error bars represent the standard deviation with respect to the mean.

target, such that there was higher precision for more recent items ($r^{\text{Pearson}} = 0.87$, 95% CI [0.82, 0.90]; $r^{\text{Spearman}} = 0.85$, 95% CI [0.79, 0.90]; Fig. 3*G*).

Together, the findings of *experiment 1* provide evidence that people can use a retrieval strategy, and not mental rotation, to successfully solve a visuomotor rotation task. In addition, we showed that retrieval is subject to capacity limitations, as reflected in larger errors, higher guessing rates, lower memory precision, and higher reaction times for longer sequences. Furthermore, we found serial position effects—a signature of working memory retrieval—where people had smaller errors, were faster, guessed less, and had more precise memories for more recent targets in the sequence. Notably, even for sequences of length 5, guessing represented a relatively low proportion of the trials (posterior mean of θ for length 5 = 0.27), which suggests that the memory capacity of participants may extend beyond five targets. In *experiment 2*, we explore this limit by exposing participants to longer sequences (larger set size).

Experiment 2

Behavioral results.

The goal of *experiment 2* was to explore the limits of visuomotor retrieval beyond the sequence lengths tested in *experiment 1*. Specifically, we sought to replicate our findings for sequences up to five targets and to assess whether the trends in our relevant variables (unsigned errors, RTs, guessing rate, and memory precision) would extend to sequences of up to 10 targets.

As in *experiment 1*, we found a significant positive correlation between the adapted magnitude and the rotation

magnitude [$r^{\text{Pearson}}(154) = 0.76$, $P < 0.001$; $r^{\text{Spearman}}(154) = 0.78$, $P < 0.001$; Fig. 2*E*], confirming that participants successfully reached the subsequent target in the sequence, and therefore counteracted the rotation. In addition, we found that participants' accuracy decreased when they faced more targets, as reflected in larger unsigned errors for longer sequences [$r^{\text{Pearson}}(115) = 0.74$, $P < 0.001$; $r^{\text{Spearman}}(115) = 0.75$, $P < 0.001$; Fig. 2*F*]. Interestingly, when we compared the unsigned errors between *experiment 1* and *experiment 2* over the same sequence lengths (2–5 targets), we found that participants from *experiment 2* performed significantly worse. This difference was tested using 2 × 4 repeated-measures ANOVA, having the experiment number and sequence length as factors and revealing a significant main effect of the experiment number [$F(1,104) = 16.31$, $P < 0.001$, $\eta^2 = 0.08$].

Similar to *experiment 1*, RTs linearly increased with sequence length [$\beta = 0.02$, $P = 0.006$, $R^2 = 0.06$, $F(1,115) = 7.68$; Fig. 2*G*] but not rotation magnitude [$\beta = 0.006$, $P = 0.68$, $R^2 = 0.002$, $F(1,76) = 0.16$; Fig. 2*H*], supporting a memory retrieval strategy instead of mental rotation. A linear regression analysis over RTs performed at the individual level also revealed that the coefficient for sequence length was significantly greater than zero [$t(12) = 2.97$, $P < 0.05$; Supplemental Fig. S1*A*]. In addition, we found that participants in *experiment 2* had significantly higher RTs than participants in *experiment 1* over the same sequence lengths (2–5 targets). This difference was assessed using 2 × 4 repeated-measures ANOVA, including experiment number and sequence length as the factors and finding a significant main effect of the experiment number [$F(1,104) = 5.41$, $P = 0.02$, $\eta^2 = 0.035$].

Corroborating the serial position effects of *experiment 1,* we found that participants had smaller unsigned errors [$r^{\text{Pearson}}(112) = -0.56$, $P < 0.001$; $r^{\text{Spearman}}(112) = -0.56$, $P < 0.001$; Supplemental Fig. S2B] and lower RTs [$r^{\text{Pearson}}(112) = -0.31$, $P < 0.001$; $r^{\text{Spearman}}(112) = -0.28$, $P = 0.002$; Supplemental Fig. S2F] for more recent targets in the sequence. We can observe a similar serial position effect in the target error distributions (Supplemental Fig. S3).

Modeling results.

Following the logic of *experiment 1,* we analyzed the source of the target errors (Fig. 3B) using a Bayesian latent-mixture model. Again, we found that the guessing rate θ increased with the sequence length ($r^{\text{Pearson}} = 0.96$, 95% CI [0.95, 0.96]; $r^{\text{Spearman}} = 0.96$, 95% CI [0.95, 0.97]; Fig. 3D); this time following a sigmoidal-like shape. Furthermore, we found that guessing became predominant (occurring >50% of the trials) for sequences above length five, which was estimated by fitting a sigmoidal function (*f*) to the posterior means (blue dots) of Fig. 3D and later computing $f^{-1}(0.5)$, which estimated 5.6 targets (Supplemental Fig. S4A). Similarly, based on the function (*f*), we found that the asymptote of the guessing rate (θ) was at 0.74. Regarding memory precision (κ), we found a negative correlation with the sequence length ($r^{\text{Pearson}} = -0.70$, 95% CI [−0.61, −0.77]; $r^{\text{Spearman}} = -0.70$, [−0.62, −0.77]; Fig. 3E), confirming the decay in memory precision with the sequence length of *experiment 1.* In addition, by visual inspection, we corroborated the behavioral differences between *experiment 1* and *experiment 2,* showing that participants from *experiment 2* performed worse over the same sequence lengths: they guessed more and had less precise memories in target sequences with two to five targets (Fig. 3, D–G).

Finally, we performed our mixture analysis to identify serial position effects, finding a negative correlation between the guessing rate θ and the position of the target in the sequence ($r^{\text{Pearson}} = -0.81$, 95% CI [−0.77, −0.85]; $r^{\text{Spearman}} = -0.77$, [−0.72, −0.82]; Fig. 3F), indicating that people guess less for the most recent items across all sequences (recency effect) as in *experiment 1.* In addition, we found a positive correlation between memory precision κ and the sequence length ($r^{\text{Pearson}} = 0.68$, 95% CI [0.61, 0.74]; $r^{\text{Spearman}} = 0.64$, 95% CI [0.57, 0.71]; Fig. 3G), suggesting that they had more precise memories for more recent items.

In summary, the results of *experiment 2* corroborated the main findings of *experiment 1* regarding the memory constraints of visuomotor retrieval strategies. Participants had larger errors, had higher RTs, guessed more, and had less precise memories for longer sequences. In addition, we confirmed a recency effect in unsigned errors, RTs, guessing rate, and the memory precision. As in *experiment 1,* we found no evidence that the participants were performing mental rotation. Interestingly, however, participants in *experiment 2* performed significantly worse than participants in *experiment 1* over the same sequence lengths according to behavioral and model-based measures, which may be a result of generally higher task demands for longer sequences. Finally, we found that the asymptote of guessing was 74% of the trials and that guessing began to dominate performance (occurring >50% of the trials) for sequences above five targets.

The goal of *experiments 1* and *2* was to embed a visuomotor rotation into the item-recognition task of Pellizzer and Georgopoulos (17) to verify the ability of retrieval strategies to solve a visuomotor rotation task. Admittedly, the designs of *experiments 1* and *2* depart from what is typically required in a visuomotor rotation task. Nonetheless, they serve as a bridge to study working-memory constraints for a retrieval strategy in a more standard visuomotor rotation task, which we systematically build toward in the following set of studies.

Experiment 3

Behavioral results.

The goal of this experiment was to estimate the working memory capacity and precision of a retrieval strategy in a task that is a step closer to a standard visuomotor rotation task. In this experiment, we implemented a trial-pair design (16; Fig. 1B) where participants ($n = 15$) were first asked to reach toward a single target location, always at 90°, and observe a cursor rotation. In the following trial, they were tasked with counteracting the rotation, therefore making the cursor hit the target. Participants were exposed to sequences of such trial-pairs with lengths ranging from one to five pairs (i.e., set size). Importantly, each pair was associated with a unique rotation that was indicated with a distinctive target color—a common dimension studied in spatial working memory. The rotations could take the values of ±30, ±60, or ±90. At the end of the sequence presentation, there was a memory test where one of the colored targets from the observed sequence was presented and participants had to counteract the rotation associated with it. Following each memory test, the associations between the color of the targets and rotation magnitudes were changed (see MATERIALS AND METHODS for details).

Similar to the visuomotor item-recognition studies, we found that in the memory test, participants successfully counteracted the rotations, as observed in a positive correlation between the adapted magnitude and the rotation magnitude [$r^{\text{Pearson}}(43) = 0.82$, $P < 0.001$; $r^{\text{Spearman}}(43) = 0.83$, $P < 0.001$; Fig. 4A]. However, participants had larger unsigned errors for longer sequences [$r^{\text{Pearson}}(73) = 0.64$, $P < 0.001$; $r^{\text{Spearman}}(73) = 0.64$, $P < 0.001$; Fig. 4B]. As in the earlier item-recognition tasks, we found that RTs linearly increased with the sequence length [β = 0.22, $P < 0.001$, $R^2 = 0.25$, $F(1,73) = 24.5$; Fig. 4C] but not the rotation magnitude [β = −0.08, $P = 0.43$, $R^2 = 0.01$, $F(1,43) = 0.61$; Fig. 4D], indicating that participants did not perform mental rotation but memory retrieval. We performed a linear regression analysis at the individual level, which also revealed that the coefficient for sequence length was significantly greater than zero [$t(14) = 5.33$, $P < 0.001$; Supplemental Fig. S1A]. In addition, we found serial position effects where participants had smaller errors [$r^{\text{Pearson}}(73) = -0.57$, $P < 0.001$; $r^{\text{Spearman}}(73) = -0.56$, $P < 0.001$; Supplemental Fig. S2C] and lower RTs [$r^{\text{Pearson}}(73) = -0.25$, $P = 0.02$; $r^{\text{Spearman}}(73) = -0.32$, $P = 0.004$; Supplemental Fig. S2G] for more recent targets in the sequence.

Modeling results.

We separated the source of the target errors (Fig. 5A) using the same Bayesian latent-mixture analysis as in *experiment 1* and *experiment 2.* Similarly, we found that the guessing rate θ increased for longer sequences ($r^{\text{Pearson}} = 0.94$, 95% CI
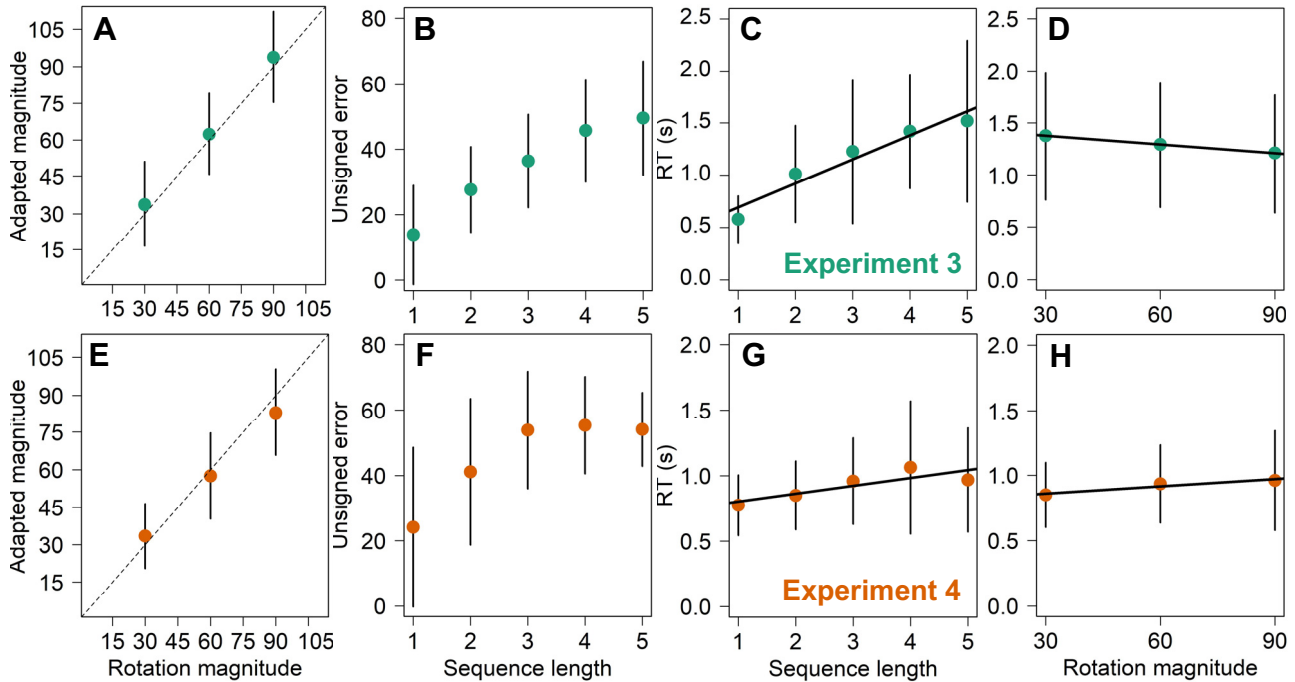
Figure 4. Behavioral results of *experiment 3* (green) and *experiment 4* (orange). *A* and *E*: per-subject mean of adapted magnitude for each rotation magnitude. The dashed lines indicate performance when perfectly counteracting the rotation. *B* and *F*: per-subject mean of unsigned errors for each sequence length. *C* and *G*: per-subject median of reaction times for each sequence length. *D* and *H*: per-subject median of reaction times for each rotation magnitude. Black solid lines show the linear models fitted to the data. Error bars represent the standard deviation with respect to the mean.

[0.92, 0.95]; $r^{Spearman}$ = 0.95, [0.93, 0.96]; Fig. 5*B*), whereas the memory precision κ decreased ($r^{Pearson}$ = −0.85, 95% CI [−0.80, −0.89]; $r^{Spearman}$ = −0.88, [−0.84, −0.91]; Fig. 5*C*). In addition, by fitting a linear model, f, to the posterior means of Fig. 5*B*, we found that guessing began to dominate performance (>50% of trials) for sequences above four targets—specifically, $f^{-1}(0.5)$ = 4.16 (Supplemental Fig. S4*B*). Furthermore, we found serial position effects, where participants guessed less ($r^{Pearson}$ = −0.85, 95% CI [−0.81, −0.88]; $r^{Spearman}$ = −0.83, [−0.78, −0.88]; Fig. 5*D*) and had more precise memories ($r^{Pearson}$ = 0.78, 95% CI [0.73, 0.83]; $r^{Spearman}$ = 0.76, [0.69, 0.83]; Supplemental Fig. S5*A*) for more recent targets in the sequence.

Overall, the results from *experiment 3* corroborate the main results in the visuomotor item-recognition tasks from *experiment 1* and *experiment 2* but in a task design that is a step closer to a standard visuomotor rotation task. In summary, we found that memory retrieval is constrained by the capacity of working memory, as shown in larger unsigned errors, higher RTs, more guessing, and lower memory precision for longer sequences. As in the visuomotor item-recognition task, we found no evidence that participants were performing mental rotation. Furthermore, we observed serial position effects both in our behavioral and model-based measures. Notably, in this experiment, guessing becomes predominant for
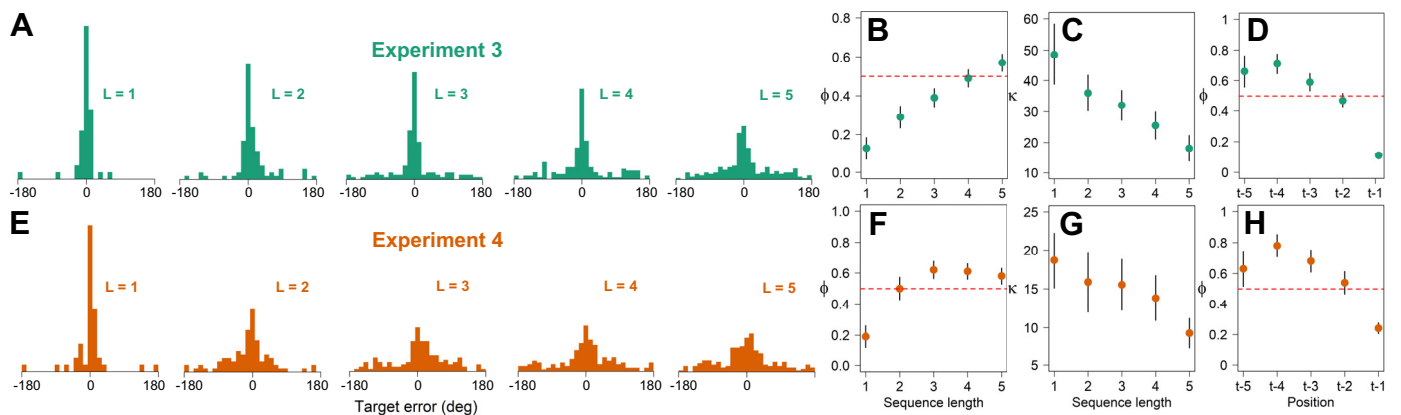

Figure 5. Modeling results of *experiment 3* (green) and *experiment 4* (orange). *A* and *E*: pooled target error distributions for each sequence length. *B* and *F*: posterior distribution of the group guessing rate parameter, ϕ, for each sequence length. The red dashed line indicates $\phi = 0.5$. *C* and *G*: posterior distribution of the group memory precision parameter, κ, for each sequence length. *D* and *H*: posterior distribution of the group guessing rate, ϕ, for the last ($t − 1$), second to last ($t − 2$), and so on, targets across sequence lengths. Error bars represent the standard deviation with respect to the mean.

sequence lengths above four targets, a capacity similar to the item-recognition task of *experiment 2*.

In the following studies, we focused on memory retrieval associated with the target location instead of target color, a design that is more common in visuomotor rotation tasks.

Experiment 4

Behavioral results.

The goal of this experiment was to provide further evidence of the constraints of working memory retrieval in visuomotor rotation tasks; this time, by making participants associate rotation magnitudes with distinct target locations instead of colors. Associating rotation magnitudes with distinct target location has been used before on dual adaptation experiments (47) as well as in trial-pair tasks (16). The target locations for every trial were randomly sampled without replacement out of eight possible values ranging from $0°$ to $315°$ in steps of $45°$. We used the same rotation magnitudes as in *experiment 3*.

As expected from our previous experiments, participants were able to successfully counteract the rotation, indicated by a significantly positive correlation between the adapted magnitude and the rotation magnitude [$r^{Pearson}(43) = 0.79$, $P < 0.001$; $r^{Spearman}(43) = 0.81$, $P < 0.001$; Fig. 4*E*]. In addition, they had larger unsigned errors for longer sequence lengths [$r^{Pearson}(73) = 0.48$, $P < 0.001$; $r^{Spearman}(73) = 0.44$, $P < 0.001$; Fig. 4*F*]. Interestingly, participants in this experiment performed significantly worse than participants in *experiment 3* (i.e., color cues), as indicated by a 2×5 repeated-measures ANOVA over unsigned errors, including experiment number and sequence length as the factors and finding a significant main effect of the experiment number [$F(1,140) = 15.9$, $P < 0.001$, $\eta^2 = 0.06$].

In addition, we found that RTs linearly increased with the sequence length [$\beta = 0.06$, $P = 0.04$, $R^2 = 0.05$, $F(1,73) = 4.28$; Fig. 4*G*] but not rotation magnitude [$\beta = 0.05$, $P = 0.33$, $R^2 = 0.02$, $F(1,43) = 0.95$; Fig. 4*H*], supporting memory retrieval over mental rotation. To corroborate these findings, we performed a linear regression analysis over RTs at the individual level, which also revealed that the coefficient for sequence length was significantly greater than zero [$t(12) = 2.49$, $P < 0.05$; Supplemental Fig. S1*A*].

Finally, we also found serial position effects where participants had smaller errors [$r^{Pearson}(73) = -0.39$, $P < 0.001$; $r^{Spearman}(73) = -0.39$, $P < 0.001$; Supplemental Fig. S2*D*] and marginally lower RTs [$r^{Pearson}(73) = -0.22$, $P = 0.05$; $r^{Spearman}(73) = -0.20$, $P = 0.07$; Supplemental Fig. S2*H*] for more recent targets in the sequence.

Modeling results.

When performing the Bayesian latent-mixture analysis to the target error distributions (Fig. 5*E*), we found that the guessing rate was higher ($r^{Pearson} = 0.73$, 95% CI [0.69, 0.77]; $r^{Spearman} = 0.64$, [0.56, 0.71]; Fig. 5*F*), whereas the memory precision was lower for longer sequences ($r^{Pearson} = -0.66$, 95% CI [−0.57, −0.75]; $r^{Spearman} = -0.67$, [−0.58, −0.76]; Fig. 5*G*); both results are consistent with our previous experiments. To know when guessing behavior began to dominate participants' performance (occurring >50% of the trials), we fitted a polynomial function, f, to the posterior means of Fig. 5*F*. Supporting the behavioral differences between

experiment 3 and *experiment 4*, we found that the guessing rate was greater than 50% of the trials starting from sequences of length 2 [$f^{-1}(0.5) = 1.98$; Supplemental Fig. S4*C*]; a noticeable reduction in capacity compared with *experiment 3*, where this value was around four targets.

As in our previous experiments, there was a recency effect in the guessing rate θ and memory precision κ, where participants guessed less ($r^{Pearson} = -0.71$, 95% CI [−0.64, −0.78]; $r^{Spearman} = -0.66$, [−0.58, −0.74]; Fig. 5*H*) and had, weakly, more precise memories ($r^{Pearson} = 0.21$, 95% CI [0.08, 0.33]; $r^{Spearman} = 0.15$, [0.05, 0.24]; Supplemental Fig. S5*B*) for more recent items, although primarily for the most recent item.

Overall, in *experiment 4*, we were able to corroborate the main findings from our previous studies where participants' performance decreased for longer sequences. However, compared with *experiment 3*, where people associated rotation magnitudes to colors, in this experiment, participants performed significantly worse, displaying a limited working memory capacity where guessing dominated performance starting from sequences of two targets. This finding would place a relatively low upper bound on how useful retrieval strategies can be for counteracting a visuomotor perturbation. Most visuomotor adaptation studies require participants to train at more target locations; however, the relationship between the target location and the rotation typically does not change from trial-to-trial, as in our trial-pair task. As such, participants experience many repetitions of the same stimulus-response association over the course of training, which would provide ample opportunity to store these associations for later retrieval according to the instance theory of automatization (28). In our final study, we addressed if these severe limitations in working memory capacity can be overcome, namely, by relying on a different memory storage: long-term memory.

Experiment 5

Behavioral results.

The goal of this final experiment was to test whether the retrieval strategies can overcome the limitations of working memory through repetition and, as such, long-term memory. To test this, participants ($n = 15$) performed the trial-pair task as in *experiment 4*; however, here they were exposed to sequences of five pairs, which would exceed our estimates of working memory capacity. Importantly, in contrast with *experiment 4*, the rotation magnitudes associated with the target locations remained the same throughout the experiment, but the order of the rotation-target pairs was randomized. This design allowed participants to experience the rotation-target associations multiple times, therefore, increasing the likelihood that they would be stored in long-term memory.

As in our previous experiments, we found that participants' performance remained highly accurate across rotation magnitudes [$r^{Pearson}(43) = 0.96$, $P < 0.001$; $r^{Spearman}(43) = 0.94$, $P < 0.001$; Fig. 6*A*]. In addition, we observed that unsigned errors [$r^{Pearson}(103) = -0.39$, $P < 0.001$; $r^{Spearman}(103) = -0.47$, $P < 0.001$; Fig. 6*B*] and RTs [$r^{Pearson}(103) = -0.33$, $P < 0.001$; $r^{Spearman}(103) = -0.26$, $P = 0.007$; Supplemental Fig. S6*A*] decreased over time, as expected, indicating that memory retrieval improves with practice. Finally, we found that RTs did not change with the rotation magnitude [$\beta = 0.06$, $P = 0.53$,
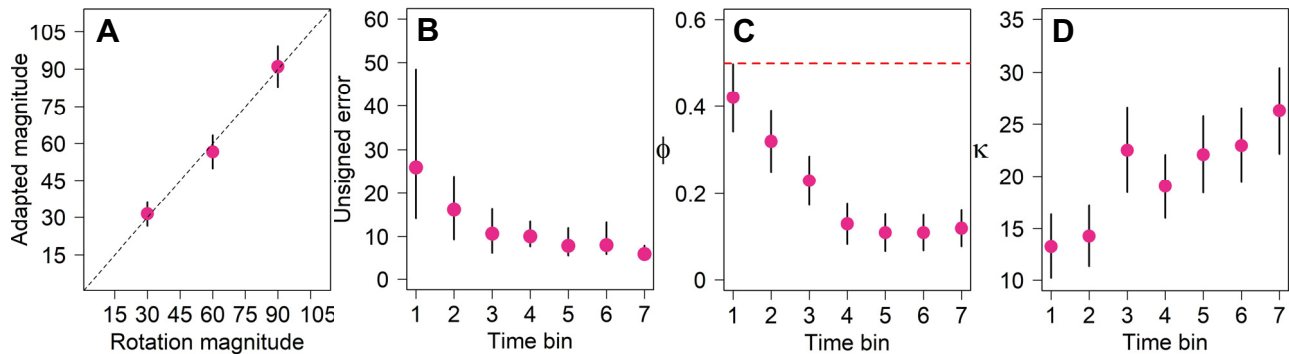
Figure 6. Behavioral and modeling results of *experiments 5*. *A*: per-subject mean of adapted magnitude for each rotation magnitude. The dashed lines indicate performance when perfectly counteracting the rotation. *B*: per-subject mean of unsigned errors over time-bins. *C*: posterior distribution of the group guessing rate parameter, ϕ, over time bins. The red dashed line indicates $\phi = 0.5$. *D*: posterior distribution of the group memory precision parameter, κ, over time bins. Error bars represent the standard deviation with respect to the mean, except for (*B*) where error bars represent the interquartile range around the median due to non-normality of the data.

$R^2 = 0.008$, $F(1,43) = 0.38$; Supplemental Fig. S6*B*], ruling out mental rotation.

Modeling results.

Corroborating our behavioral findings, we found that the guessing rate θ decreased over time ($r^{\text{Pearson}} = -0.81$, 95% CI $[-0.78, -0.84]$; $r^{\text{Spearman}} = -0.79$, $[-0.74, -0.84]$; Fig. 6*C*), reaching a posterior mean of 12% of guessing by the end of the experiment. Notably, this value is lower than the guessing rate for sequences of a single target (i.e., the smallest set size) in *experiment 4* (posterior mean of θ for sequence length 1 = 19%). Similarly, the memory precision κ increased over time ($r^{\text{Pearson}} = 0.70$, 95% CI $[0.62, 0.77]$; $r^{\text{Spearman}} = 0.71$, $[0.63, 0.77]$; Fig. 6*D*), reaching a posterior mean of $\kappa = 26$ by the end of the experiment, which is higher than the precision of target sequences of length 1 in *experiment 4* (posterior mean of κ for sequence length 1 = 13).

In summary, the results of *experiment 5* showed that the capacity limitations shown in *experiment 4* can be overcome over time, at a point where performance is better than in the shortest sequence relying on working memory.

Model Comparison

To validate the results from the Bayesian latent-mixture model, we compared its performance with a model that assumed that target errors had a single source, namely, the memory (Von Mises) distribution. We found that qualitatively and quantitatively—using leave-one-out cross validation (52, 53)—the Bayesian latent-mixture model outperforms the single-source model in all experiments and sequence lengths (Supplemental Fig. S7).

◼ DISCUSSION

Summary

Through a series of studies, we showed that participants can effectively use retrieval from memory as a strategy for visuomotor adaptation. From *experiment 1* to *experiment 4*, we found key signatures of working memory retrieval, namely, lower accuracy and higher RTs as the number of targets in the training set increases (set size; 25, 39, 45, 57, 58). In addition, we found a recency effect where participants

were more accurate and had lower RTs for more recent items, also a seminal finding in working memory studies (25, 58). These behavioral results were supported by group model-based metrics, which revealed that participants were guessing more and had less precise memories for longer sequences (i.e., larger set size), as well as less guessing and more precise memories for more recent items—a recency effect. *Experiment 5* revealed that these apparent working memory limitations could be overcome with repetition, suggesting that retrieval strategies can also rely on long-term memory. This later finding is consistent with the instance-based theory of automatization and may provide clues as to how a strategy could lead to skill development (28).

Capacity Limitations of Retrieval Strategies

From our model-based analysis, we found that guessing behavior began to dominate participants' performance (more than 50% of trials) in the visuomotor item-recognition task for training sets beyond five targets, and similarly for the visuomotor rotation recall task with color cues, for sets beyond four targets. Both of these performance thresholds are similar to the capacity limitations documented in previous studies (59, 60). Interestingly, we found that for *experiment 4*, where visuomotor rotation recall was based on location cues, guessing exceeded 50% of trials starting with sequences of two targets, which was a striking reduction in performance. Although previous work has shown that both colors and locations can serve as contextual cues when adaptation is primarily driven by an explicit strategy (61, 62), differences in their effectiveness in cueing a rotation in our experiments might be due to the fact that, although both spatial locations and colors are continuous variables, colors are typically associated with well-known categories (red, green, purple, etc.), requiring minimal or no learning. On the contrary, target locations were not explicitly linked with well-known categories in space; therefore, participants probably had to memorize the target locations as well as the rotation magnitude associated with them. Future experiments could test this hypothesis, for example, by providing clock "marks," around the ring, indicating the locations where the target could appear. This way, participants can use a well-known reference frame to remember the target locations

(e.g., target at 6 linked with 90° rotation). We would expect that in this scenario, performance would be similar to *experiment 3*.

In addition, it is worth noticing that we found significant differences in performance between the two studies in the visuomotor item-recognition task. Specifically, in *experiment 2*, participants showed overall lower performance, both in behavioral and model-based metrics, as compared with participants in *experiment 1* over the same set sizes. Since participants in *experiment 2* were additionally presented with sets greater than 5 and up to 10 targets, we credit this effect to a higher cognitive load imposed by the average set size in the experiment. This decrease in performance has been reported before in working-memory studies, although usually when participants perform a distracting task either from the same or a different domain (63).

It has been widely debated whether human working memory is better described by models that assume a fixed-slot or a continuous resource capacity (42, 64). Whereas the original form of the fixed-slot models would assume a shift from retrieval to guessing after memory capacity is surpassed, the continuous resource models predict, instead, a decline in the memory precision as the number of items to be remembered increases. Using the Bayesian latent-mixture model, we allowed for the incorporation of both of these assumptions. In particular, target errors were modeled as a combination of memory (Von Mises) distribution and a guessing (uniform) distribution; at the same time, we allow the memory precision to be variable across set sizes. Interestingly, we found qualitative and quantitative evidence (Supplemental Fig. S7) that the decrease in participants' performance was the result of a combination of both increased guessing and decreased memory precision, which is consistent with both frameworks. However, we did not find abrupt changes on participants' performance, particularly in *experiment 2*, where target sequences far exceeded typical capacity thresholds, which would be predicted by an all-or-none, fixed-slot model (41). Instead, unsigned errors, guessing rate, and memory precision seem to describe continuous functions, results that better align with the predictions of continuous resource models (64, 65). Further work would be necessary to assess whether other instances of continuous resource models, e.g., that assume a different precision per trial (64), can provide a better description of this data set without the assumption of a guessing distribution.

Finally, we should note that we view these working-memory capacity limitations as arising from limits in visuospatial working memory, given the remarkable similarity in our findings with studies of visual short-term memory in domains outside of motor control (23–26, 42). This perhaps is not surprising since the reaching movements in our task were ballistic and visual feedback of the cursor was delayed to prevent implicit recalibration. Although it is possible that proprioception or somatosensory information could be leveraged to recall a successful reach location with a specific target location (66, 67), the most salient features of the task were visuospatial—target and planned aiming location. Retrieval strategies could differentially rely on visuospatial and somatosensory "motor working memory," which appear to be dissociable (68), depending on the nature of the task. However, the absence of aftereffects during the washout phase in all our experiments suggests that performance was primarily based on explicit processes (Supplemental Fig. S8).

Retrieval versus Algorithmic Strategies

In recent years, experimental work on visuomotor adaptation has revealed that people can deploy at least two kinds of cognitive strategies in response to feedback perturbations. Algorithmic strategies, which allow for the discovery of generalizable aiming solutions, are computationally demanding. On the contrary, memory retrieval allows for a fast and computationally effective way to recover known aiming solutions but is limited in generalization and capacity. Previous work has shown that participants can switch from algorithmic to retrieval strategies as the experimental session progresses, which is reflected in a decrease in RTs over time (16). This transition is consistent with a process of automatization and memory consolidation characteristic of the development of a skill (28).

Although retrieval strategies can convey an advantage in computational cost reflected in a reduction in RTs, this benefit is likely to become more evident as the aiming solutions are consolidated into long-term memory due to repetition. Indeed, in the study by McDougle and Taylor (16), RTs differences between participants performing algorithmic and retrieval strategies are accentuated as the aiming solutions are repeated over the experimental session. This enhancement in computational efficiency is analogous to the one of mental arithmetic (22), where the solutions for common operations are readily retrieved from memory (e.g., the result of 5 times 5), whereas the solutions for less common, or novel, operations are more slowly performed algorithmically (e.g., the result of 23 times 11). We observed a similar improvement in computational efficiency in *experiment 5*, where RTs, unsigned errors, and guessing decreased, whereas memory precision increased, with more repetitions of the aiming solutions. However, this improvement was most likely driven by a transition from working memory to long-term retrieval and not from algorithmic computations to long-term retrieval, as we found no evidence of mental rotation in the experiment (Supplemental Fig. S6*B*).

However, when the aiming solutions are presented a single time as in *experiments 1–4*, the computational efficiency gained through repetition is not attainable. In this scenario, where retrieval relies instead on working memory, the computational cost can increase as more solutions have to be stored. Evidence for this idea is found in previous work (17, 39, 45) as well as in the present studies, where RTs linearly increase with the set size, which has been proposed to be the consequence of a scanning process over the items in memory (39, 45, 69). Notably, this linear increase in RT with set size in memory-based retrieval tasks mirrors the linear increase in RT with rotation magnitude in mental rotation tasks. However, there is substantial evidence suggesting that they are the result of fundamentally different psychological and neural operations (16, 17, 70).

Whether memory scanning is computationally cheaper than mental rotation is an open question. From the set of studies we have presented, *experiment 4* has the most comparable design to the McDougle and Taylor (16) trial-pair rotation task, where the linear relation between RTs and rotation magnitudes was documented. Specifically, both

designs vary the target location on which the aiming solution is tested. In our *experiment 4*, participants reached RTs medians of around 1 s for the longest target sequences, which is around the RT values for the smallest rotations in McDougle and Taylor (16), and where the largest rotations reached values of around 1.3 s. This would suggest that retrieval, even when it occurs from working memory, could be computationally cheaper than mental rotation. However, an experiment that evaluated these comparable designs could provide empirical evidence of the computational efficiency of each strategy.

Automatization of a Skill

It is well known that practice generally leads to task improvements in terms of speed and accuracy (71). One potential explanation for this improvement is the increased efficiency of algorithmic processes (e.g., that mental rotation is performed faster and more accurately over time) and reflected in transfer effects to new stimuli. Crucially, to the authors' knowledge, there is mixed evidence that such transfer occurs (30, 31). However, a recent study by Provost et al. (72) found out that the speed of mental rotation can indeed improve, and therefore be reflected in transfer, but only when participants are trained with a large stimulus set. On the contrary, when McDougle and Taylor (16) trained participants to counteract 12 different rotations associated with different targets, which favors the use of mental rotation over memory retrieval due to capacity limitations, their RTs only gently decreased with training, suggesting that participants continued using mental rotation with the same efficiency throughout the task. Although further research is needed to understand whether algorithmic processes can improve with practice, this route of improvement was unlikely to occur in our studies, particularly in *experiment 5*, as we found no evidence of mental rotation in the first place.

However, it has been proposed that, when developing a new skill, people start by relying on algorithmic strategies but subsequently transition to perform memory retrieval of already known solutions (28)—with this transition entailing a reduction in the computational cost. Although this process likely underlies a wide variety of human skills like mental arithmetic, we found evidence that long-term retrieval does not need to be preceded by algorithmic performance. Instead, it can result from consolidating task solutions that had already been stored in working memory. We can think, for example, that in a pool game, a player can temporarily store the shooting locations that were verbally or visually conveyed by a more experienced player without having to compute them themselves. These solutions, if successful, can be consolidated for future use into long-term storage. Such a strategy can prove successful in the short-term, only relying on algorithmic performance in the absence of temporarily stored solutions, such as in the presence of novel stimuli (73).

However, when the task at hand has no explicit incentive to use retrieval right from the beginning (as in our studies), a more natural transition in the development of a skill could be starting with algorithmic processes, followed by working memory retrieval and long-term retrieval if the solutions are consolidated (74). The inability to transition from algorithmic to retrieval strategies when working memory capacity is

exceeded (16) highlights the relevance for the study of the latter to understand the successful acquisition of visuomotor skills.

Further insight about the role of working memory in motor learning can be gained from studies on value-based decision making (33). For example, previous research has suggested that working memory can support decisions by holding information about rewards (75) or transfer knowledge across tasks (76). Similarly, when the stimulus set that participants have to learn from is small, decisions seem to be dominated by working memory information, whereas for larger sets, incremental learning prevails (32). Therefore, it is conceivable that working memory has a similar relation with error-driven processes in motor learning. For example, in motor adaptation tasks where the number of rotations to be learned is small, working memory can serve as a temporary storage for those solutions, whereas for longer set sizes, error-driven processes might dominate.

Overall, this work opens future avenues of research where other memories, such as episodic memories (34, 35, 77), can be the subject of study as potential sources of visuomotor solutions for adaptation.

DATA AVAILABILITY

Data, code, and supplemental figures from the studies reported in this manuscript are available at https://osf.io/z3cua/.

SUPPLEMENTAL DATA

Supplemental Figs. S1–S8: https://osf.io/z3cua/.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

C.A.V.-V. and J.A.T. conceived and designed research; C.A.V.-V. performed experiments; C.A.V.-V. analyzed data; C.A.V.-V. and J.A.T. interpreted results of experiments; C.A.V.-V. prepared figures; C.A.V.-V. and J.A.T. drafted manuscript; C.A.V.-V. and J.A.T. edited and revised manuscript; C.A.V.-V. and J.A.T. approved final version of manuscript.

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