Visuomotor adaptation via featureless objects

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Abstract

Implicit visuomotor adaptation is thought to be driven by sensory prediction errors — the difference between predicted and observed visual feedback given an outgoing motor command. But which aspects of visual feedback are relevant to implicit adaptation? In typical visuomotor adaptation tasks, visual feedback is given in the form of objects easily perceived via segmentation from the background (e.g., a white cursor on a black background). Here, we challenge the idea that such segmentable objects are a requisite visual feature for visuomotor adaptation, hypothesizing that more abstract visual representations are used to compute sensory prediction errors. We explored visuomotor adaptation using novel *featureless-object feedback*. In Experiment 1, subjects moved their cursor in a workspace tiled with blue squares of varying brightness. As they moved, each square their hand entered changed from one random shade to another. Feedback was then rotated relative to hand movements, and adaptation was measured via implicit aftereffects. Despite the lack of segmentable object features, participants adapted robustly. Indeed, in a second study we observed that the magnitude of aftereffects was even larger using the featureless-object feedback versus more conventional visual cursor feedback. In Experiment 2, we extended this finding to another form of abstract feedback: random pixel shuffling within a static background. We again observed robust implicit aftereffects, and also observed a canonical cosine-shaped spatial generalization function. Finally, in Experiment 3 we found that different forms of abstract error feedback could be linked to the same visuomotor memory: We observed complete transfer of adaptation between the brightness-change and pixel-shuffle feedback contexts. Taken together, these results suggest that error-based motor learning is sensitive to a surprisingly abstract level of visual representation — pure change that is spatiotemporally correlated with movement.

Keywords: generalization, motor learning, adaptation, motion perception, visual features

Introduction

From modifying our gait when we walk on icy pavement to making tiny adjustments to our racket grip while playing pickle-ball, we constantly and unconsciously refine our actions to match our goals. A key mechanism supporting this constant refinement process is error-based motor learning, whereby discrepancies between intended actions and sensory consequences — known as sensory prediction errors (SPEs) — signal the need for automatic, implicit behavioral adjustments. SPEs arise when predicted sensory outcomes differ from actual sensory feedback from a motor command, an error signal which the brain uses to recalibrate motor output to better align actions and predicted sensations [1].

Among the different types of sensory input available to the motor adaptation system, visual feedback plays a prominent role. However, the precise visual properties that are necessary or sufficient for triggering implicit motor adaptation remain unclear. Visuomotor adaptation is typically studied in paradigms such as visuomotor rotation learning (VMR) tasks [2], where feedback typically takes the form of a cursor or similar object acting as a visual proxy of the participant's hand. This feedback can be perturbed to drive adaptation by imposing an angular rotation between the motion direction of reaching movements and visual feedback. Participants learn to compensate to such perturbations by unconsciously and incrementally reaching in the opposite direction of the perturbation over repeated attempts. The visual stimuli used in such experiments are typically well-defined by shape, color, and motion, and are salient visual objects that are easily segmented from the background. Because of this, it is not known what specific visual information the motor adaptation system uses to compute errors to drive learning — does it require segmentable, persistent object features, or does it rely on more abstract signals? Answering this question is key to better understanding the exact sensory inputs used by the adaptation system to drive learning, both at an algorithmic and neural level.

Despite this gap in knowledge, previous work has demonstrated the basic requirements of effective visual signals for motor adaptation. First, visual feedback must be sensed soon after a motor command is issued — if feedback is delayed relative to a movement by as little as half a second, adaptation is attenuated or even abolished [3–6]. Second, visual feedback should be reliable — adaptation is attenuated if visual feedback is noisy or uncertain, such as when a cloud of points is used as feedback instead of a discrete object [7] or if feedback is only briefly flashed at the endpoint of a movement [8–11]. These findings suggest that the timing, precision, and temporal continuity of feedback influence the degree of motor adaptation.

Yet, in contrast to these established constraints, a recent study demonstrated that the adaptation system is surprisingly insensitive to some rather salient features of visual feedback [12]. Warburton et al. found that adaptation to a visuomotor rotation was identical across two distinct contexts where the same hand movement caused visual motion in opposite directions: the movement either caused a cursor to move towards a target within a large ringed workspace (i.e., the traditional visuomotor adaptation set-up), or it caused the entire workspace to move in the opposite direction of movement, bringing the target to the hand (as in a first-person shooter video game). Critically, after adapting in one of these contexts, adaptation behavior fully transferred to the other context and vice versa. This result suggests that a rather abstract visual representation is used to drive visuomotor adaptation for a given motor command, one that is not bound to the direction of perceived visual motion, but is instead computed with respect to more abstract visual consequences of movement.

Here we build on this previous work to further understand the necessary and sufficient visual signals needed for visuomotor adaptation. Inspired by recent work about "featureless objects" [13], here we explored visuomotor adaptation using featureless object displays — in which it is never possible to segment a visual object from the background — and in which there are no enduring object properties from moment to moment. In our tasks here, visual feedback was represented by random changes of either brightness or local contrast

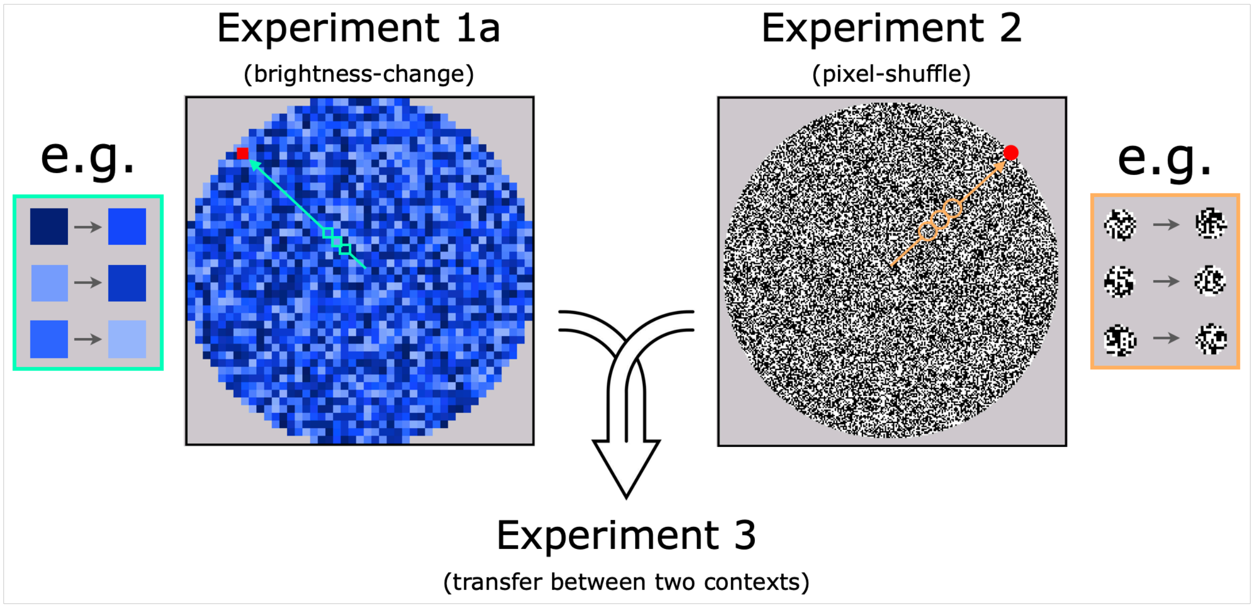

Fig. 1: Illustrations of the visual feedback used in our visuomotor rotation tasks. In Experiment 1a, participants performed center-out reaching movements in a workspace filled with hundreds of blue-shaded squares, and visual feedback of the hand position was signaled only by changing each new square they moved into from one random brightness to a different random brightness. In Experiment 2, every movement of the hand was indicated by a completely random shuffle of pixels in a small disc corresponding to hand position. Experiment 3 explored the transfer of learning between these two visual contexts. Readers can experience the tasks for themselves at: `https://zk.actlabresearch.org/featureless`

patterns that are spatiotemporally correlated with hand movements (Fig. 1). First, we examined whether perturbations to these featureless signals can produce canonical motor adaptation signatures, i.e., robust implicit aftereffects and cosine-shaped spatial generalization functions [14, 15]. Then, we used two distinct displays within a single task, asking whether visuomotor adaptation memories tied to two markedly different feedback contexts can transfer from one context to the other. This design thus allowed us to further shed light on the level of abstraction at which the visual features of sensory prediction errors are represented to drive visuomotor learning.

Methods

Open Science Practices

An archive of the data, experiment code, stimuli, and other relevant materials is available at `https://osf.io/duzh4/?view_only=1ed9b3e8eba443329125e43d9d8fb7fe`. For all experiments, we pre-registered the sample size, experimental design, exclusion criteria, and statistical analyses. Readers can find the demonstrations of the stimuli and experience the tasks for themselves at: `https://zk.actlabresearch.`

org/featureless.

Participants

As stated in our pre-registration, we recruited 50 participants for each experiment. We chose this sample size based on a smaller pilot study (n=10) for Experiment 1 that yielded similar results. We conservatively increased the sample size given the use of remote data collection. All participants were recruited online via Prolific (`https://www.prolific.co/`). For a discussion of this participant pool's reliability, see [16]). Participants were pre-screened for ages 18 - 35, a minimum approval rate of 99%, at least 50 prior submissions, normal or corrected-to-normal vision, fluency in English, and U.S. residence. This research received approval from Yale University's local ethics board, and informed consent was obtained from all participants before testing.

Stimuli and task

In Experiment 1a, the workspace was a circle with a radius of 400 pixels, tiled with blue squares of which the initial contrast intensity (i.e., the shade of blue) differed randomly across the squares on every trial (hue value: 223; saturation value: 100%; brightness value range: 20 — 80). When subjects moved in this workspace, visual feedback of their hand position was not signaled by a moving object — instead, it was signaled only by changing each new square they moved into from one random brightness value to a different random brightness value. As a result, it was never possible to see one's current hand location in any static frame, and no particular brightness change persisted from moment to moment during any movement.

At the start of each trial, participants positioned their hand in a central position with the aid of a visual disc whose radius represented the distance between the hand and the starting position. After the hand hovered over the start point, participants clicked the mouse and immediately saw a single red square target drawn from a distribution of five possible target positions arranged around the boundary of the upper half of the circular workspace (0°, 45°, 90°, 135°, 180°). Participants were asked to perform ballistic center-out-reaching movements from the center of the workspace through the target. Their reach had to cross the boundary of the circular workspace that contained the target between 100 ms to 1 s to avoid "too fast" or "too slow" warnings, respectively. (Fig. 1A).

Experiment 1a consisted of a baseline phase (40 trials), a learning phase (120 trials), and a washout phase (40 trials). During the baseline phase, participants reached to targets with non-rotated feedback to get accustomed to the reaching task. During the learning phase, feedback was rotated by 30° (the sign of the rotation was counterbalanced across participants), such that a movement trajectory through the workspace would cause a sequence of random color changes along a line of squares offset from the reach trajectory. During the washout phase, participants were instructed to stop using any deliberate strategies and reach straight to the target without any feedback, allowing us to isolate canonical implicit adaptation aftereffects [17,18]. In each phase, each of the 5 target locations were presented in a randomized order, with the same number of total repetitions for each target.

To compare the results of Experiment 1a with more typical visuomotor adaptation feedback, Experiment 1b used the same design and procedure as Experiment 1a except that discrete cursor feedback was shown as a persistent dark-blue cursor that could be easily visually segmented from the same square-tiled workspace.

In Experiment 2 we tested both adaptation in a different variant of featureless-object feedback and also spatial generalization of learning to novel target locations. The workspace consisted of a circle of static visual noise with a radius of 300 pixels. Participants moved to a red target located at the boundary of the circle, with their movement was indicated by a fully random shuffling of pixels within a small disc with a radius of 18 pixels (Fig. 1B). For each participant, a single, fixed target direction was randomly chosen from five directions (0°, 45°, 90°, 135°, 180°) at the beginning of the task (a single target location was used to afford a later generalization test). During the baseline phase, 42 trials involved reaches to 7 possible target locations (0°, ±15°, ±30°, ±60° relative to the direction of adaptation; e.g., if the adaptation target direction was 90°, then reach directions would be at 30°, 60°, 75°, 90°, 105°, 120°, 150°), with 6 reaches to each location presented in a randomized order. After this baseline phase, for 102 trials (learning phase) participants experienced a 30° rotation (the sign of rotation was counterbalanced across participants) while reaching to a single learning target location (e.g., 90°). The final 56 trials were designed to test for generalization to novel adjacent locations, in which participants reached directly to the 7 locations tested in the baseline phase without feedback.

Experiment 3 tested the transfer of visuomotor adaptation across the brightness-change context (Experiment 1) and pixel-shuffling contexts (Experiment 2). The procedure was identical to Experiment 1 except that the brightness-change workspace served as the "untrained" context and the pixel-shuffling workspace served as the "trained" context (and vice versa for a counterbalanced group). Participants first completed 20 trials in the "untrained" context followed by 20 trials in the "trained" context in the baseline phase. Next, they completed 120 learning trials in the "trained" context, with a 30° rotation applied to their feedback (direction counterbalanced across participants). Then, the perturbation was turned off and the context switched again, and participants completed 30 reaches in the "untrained" context with visual feedback removed. The final 10 trials in this washout phase was then completed back in the "trained" context.

Data analysis

We recorded mouse position (x- and y-coordinates) along each reach trajectory, from the central start point to the endpoint (when the hand passed out of the circular workspace). For Experiment 1a, we pre-registered three dependent metrics: 1) Endpoint error — the angle between the direction of the endpoint of the reaching trajectory and the direction of the target; 2) Heading error — the angle between the initial movement direction (defined as the point closest to two square cells away from the hand's starting point) and the target direction; and 3) Averaged error — the averaged angle between each point along the recorded movement trajectory and the direction of the target. Given that our results were qualitatively identical between these three metrics, we pre-registered the endpoint error as the only metric for follow-up experiments to avoid redundancy. Data from participants in the different rotation sign groups (i.e., -30 vs +30 degrees) were flipped such that the optimal reach direction for all participants was matched.

As stated in our pre-registrations, trials with extremely large errors (i.e., the endpoint of movement trajectory > 90° from the ideal angle) or missing values were excluded. On the individual level, we excluded participants who failed to submit a complete dataset, reported technical issues, had more than 10% trials excluded, or did not show any sign of learning (i.e., the averaged error of the last 5 trials in the learning phase was equal to or larger than the average error of the first 5 learning trials). (We note that no patterns reported below depended on excluding trials or individuals; i.e., all effects remained significant, in the same direction, even when all participants and trials were included in the analysis.)

We performed two-tailed paired t-tests (α=0.05) on participants' error data to examine: 1) Learning — whether the average error in the last 5 learning trials significantly decreased relative to the first 5 learning trials; and 2) Aftereffects — whether the average error in the full washout phase was significantly biased to the direction that counters the rotation, relative to the averaged error of the baseline phase. We also performed two two-sampled t-tests (α=0.05) to compare learning effects and aftereffects between featureless

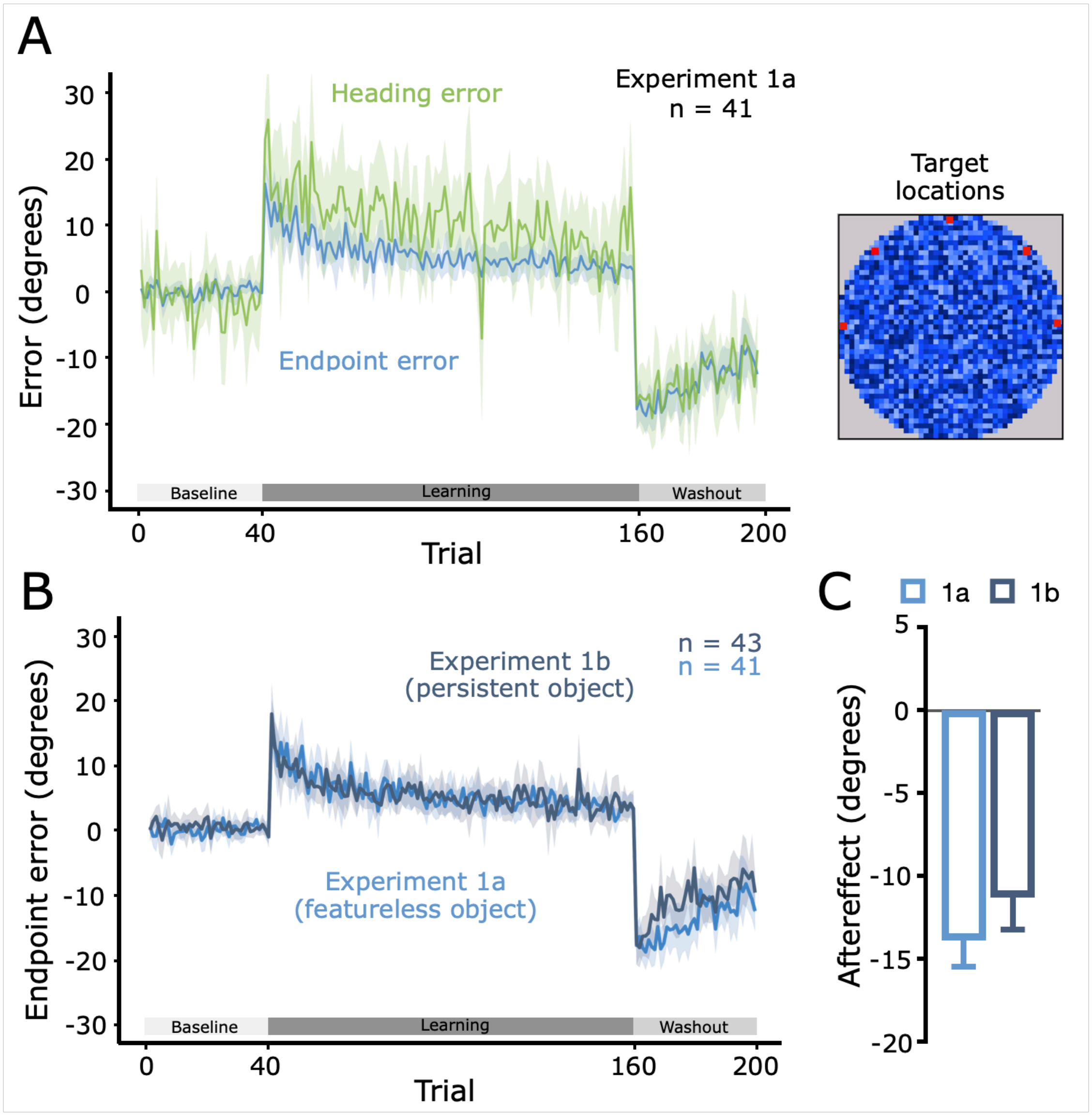

Fig. 2: Results for Experiment 1a and 1b. A: Mean angle error across all trials. Participants adapted their reach to compensate the 30° perturbation in Learning phase, and showed significant aftereffects in Washout phase. B: Featureless object versus normal object as visual feedback in motor learning. C: Between-subject difference of aftereffects in Experiment 1a and 1b. The featureless-object group showed a slightly stronger implicit adaptation ($p = 0.044$). The shaded area and vertical bars show the 95% confidence intervals.

feedback versus normal feedback (Experiment 1a versus 1b). To test generalization in Experiment 2, we fitted the error data across target locations in the generalization phase with a linear regression model with a quadratic term and Gaussian functions to estimate height, width and center parameters. Each participant's implicit generalization function was determined by calculating the mean implicit aftereffect at each of the 7 locations during Washout trials. A Gaussian function was fit to the group data via bootstrapping, resampling our subject pool with replacement 1,000 times, and its parameters were optimized to provide the lowest root mean square error (rmse) between the fitted curve and the bootstrapped mean function.

Results

Experiments 1a and 1b

In Experiment 1a, participants completed a VMR task where movement was signaled by random changes of brightness in an array of blue squares (Fig. 1A). Nine participants were excluded (1 for having ¿10% invalid trials, 1 for not showing any sign of learning, and 7 for failing to submit a complete dataset), leaving 41 participants with analyzable data. As shown in Fig. 2A, the participants' reach errors gradually decreased during the learning phase, showing that they compensated for the rotation. The mean reaching error of the first five learning trials was significantly larger than that of the last five trials (Heading angle: $MD = 7.2°$, $t(40) = 3.24$, $p = 0.0024$, Cohen's $d = 0.51$; Averaged angle: $MD = 9.9°$; $t(40) = 7.04$, $p = 1.67 \times 10^{-8}$, $d = 1.10$; Endpoint angle: $MD = 9.5°$, $t(40) = 8.34$, $p = 2.76 \times 10^{-10}$, $d = 1.30$). Critically, significant aftereffects emerged after visual feedback was removed and participants were instructed to directly reach to the targets ($t(40) = 7.04$, $p = 1.67 \times 10^{-8}$, $d = 1.10$), reflecting classic implicit visuomotor learning effects (mean endpoint angle in Washout phase: -11.21°). Thus, visual feedback of movements given via pure brightness changes that are spatiotemporally correlated with movement can signal an error and induce implicit motor adaptation.

Is adaptation weakened by this featureless-object feedback relative to more typical feedback? Or is it equivalent, or perhaps even greater? To test this, in Experiment 1b we provided participants with a persistent blue disc to represent movement, similar to typical VMR tasks. Seven participants were excluded (2 for having ¿10% invalid trials, 4 for not showing any sign of learning and 1 for failing to submit a complete dataset), leaving 43 participants with analyzable data. As predicted, participants showed significant learning effects and aftereffects (learning: $t(42) = 7.46$, $p = 3.18 \times 10^{-9}$, $d = 1.14$; aftereffect: $t(42) = 12.52$, $p = 9.09 \times 10^{-16}$, $d = 1.91$), consistent with previous findings in typical VMR tasks.

To assess differences between typical versus featureless-object visual feedback, these effects were compared to Experiment 1a. As can be seen in Fig. 2B, participants counteracted the perturbation to a similar degree during the Learning phases in Experiment 1a and 1b (error decreased by 9.5° in 1a versus 8.9° in 1b, $t(82) = 0.37$, $p = 0.71$). Surprisingly, featureless-object feedback induced stronger aftereffects than the typical feedback (13.9° versus 11.3°, $t(82) = 2.04$, $p = 0.044$, $d = 0.45$; see Fig. 2C). The results of Experiment 1 suggest that the visual system can compute visuomotor prediction errors in the absence of persistent, segmentable objects, and moreover, that abstract visual changes which are spatiotemporally correlated with movement may be necessary and sufficient for these error computations.

Experiment 2

In Experiment 2 we extended our results to a new context, where movement feedback was signaled by randomly shuffling pixels around in the area of the hand position. We also examined if and how implicit visuomotor memories spatially generalized to new movement targets when visual feedback was limited to

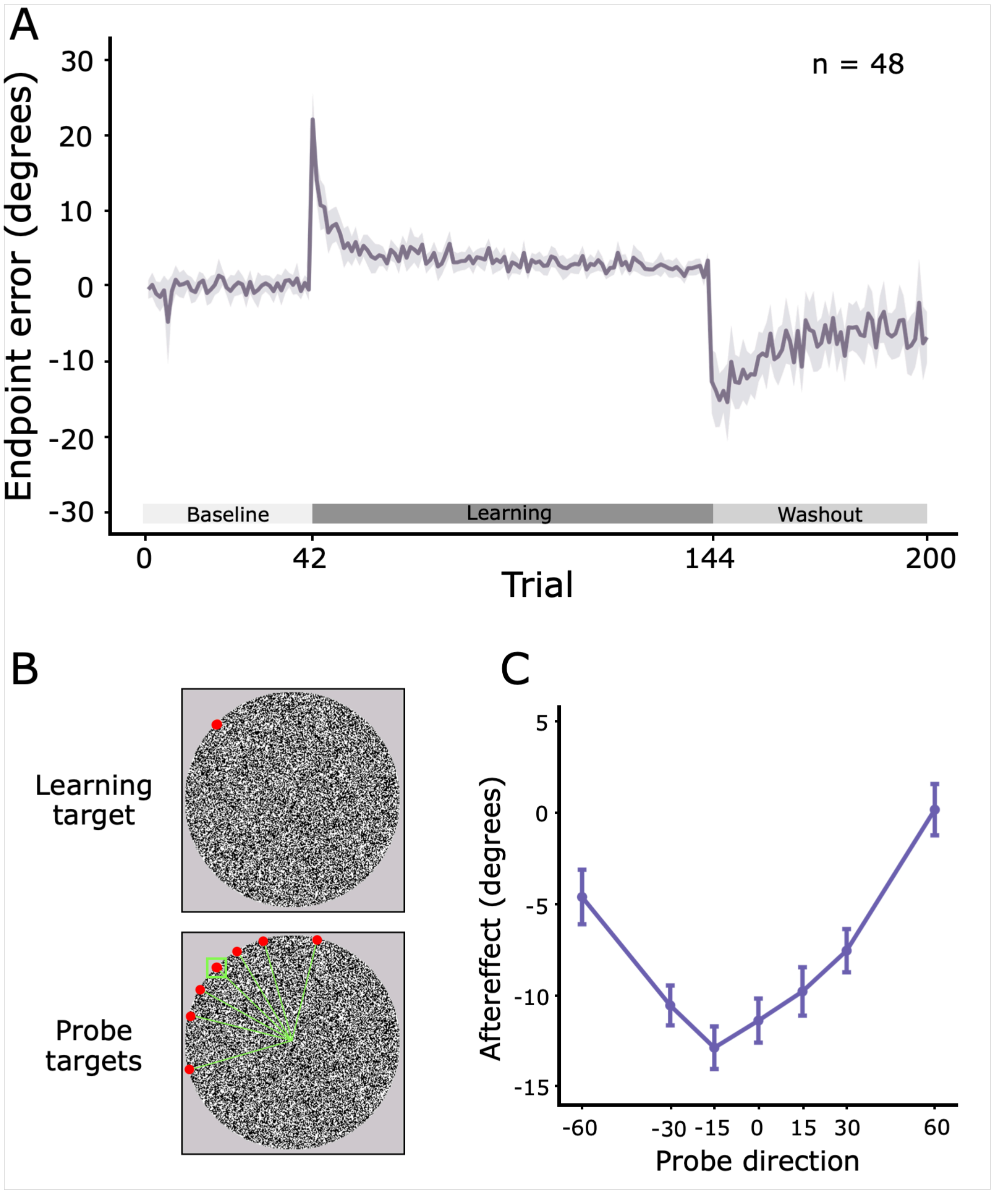

Fig. 3: Results of Experiment 3. A: Mean endpoint error of reach angle across all trials. Participants quickly counteracted 30° rotation and robustly adapted later. B: Participants reached to a single location in Learning phase and reached to seven different locations in Washout. C: Generalization of aftereffects. Learning in one location tapers off in a Gaussian-like fashion to neighboring locations. The shaded area and vertical bars show the 95% confidence intervals.

featureless objects. Two participants were excluded (1 for not showing any sign of learning and 1 for failing to submit a complete dataset), leaving 48 participants with analyzable data. Participants reached to a single target located in a fixed direction during the Learning phase, and then in the Washout phase, they reached to this adapted direction in addition to 6 adjacent directions without visual feedback (Fig. 3B).

Again, participants adapted their reaches to compensate for the rotation during the Learning phase (Endpoint error decreased by 10.2°; $t(47) = 11.37$, $p = 4.30 \times 10^{-15}$, $d = 1.64$). Replicating and extending Experiment 1, participants' also displayed robust implicit aftereffects (mean = -7.8°, $t(47) = 11.08$, $p = 1.07 \times 10^{-14}$, $d = 1.60$).

Moreover, our generalization test revealed a canonical Gaussian generalization pattern of the observed implicit learning (model fitting results: estimated height = -12.28, width = 34.45, center = -9.89). As can be seen in Fig. 3C, implicit adaptation at the probe locations decreased with increasing distance from the original learning location (A linear model revealed a significant quadratic term, $b = 0.0026$, $t = 15.55$, $p < 0.0001$). Finally, peak aftereffects were present near the -15° target, consistent with plan-based generalization [19,20].

Across Experiments 1 and 2, featureless-object visual feedback produced two canonical implicit adaptation signatures — robust aftereffects and a cosine-shaped spatial generalization function, supporting the idea that the adaptation system can compute sensory prediction errors without persistent, segment-able visual object features. This suggests that somewhat abstract perceptual features are the necessary input to the error computation process.

Experiment 3

In Experiment 3, we pushed this idea further, asking if a visuomotor memory formed in one featureless-object feedback context would transfer to another. If confirmed, such transfer would suggest that the abstract visual feature driving adaptation is not bound to the particulars of the visual scenes, and is thus a good candidate for the visual signal used to compute sensory prediction errors.

Both our brightness-change and pixel-shuffle displays were presented in Experiment 3. During the Learning phase, participants adapted to a rotational perturbation in one context ("trained" context). During Washout, they reached directly to targets without cursor feedback, but in the other context ("untrained" context), providing a contextual transfer test [12]. Three participants were excluded for no sign of learning, leaving 47 with analyzable data.

As can be seen in Fig. 4, participants showed significant learning (Endpoint error decreased by 13.5°, $t(46) = 13.10$, $p = 3.92 \times 10^{-17}$, $d = 1.91$). Crucially, during the Washout transfer phase we observed robust implicit aftereffects ($mean = -13.1°$, $t(46) = 17.82$, $p = 2.82 \times 10^{-22}$, $d = 2.60$). This result demonstrates that visuomotor adaptation obtained in the trained context fully transferred to the untrained context. These results further suggest that the error computation is not sensitive to persistent visual features, discrete objects, or holistic scenes, but rather it uses abstract visual representations to compute prediction errors and create and adapt visuomotor memories.

General Discussion

What visual features drive visuomotor adaptation? In typical adaptation tasks, sensory prediction errors (SPEs) are informed by a salient, persistent proxy of an effector (e.g., a cursor representing the hand) moving in an unexpected way. In such cases, the adaptation system must continuously track certain visual features

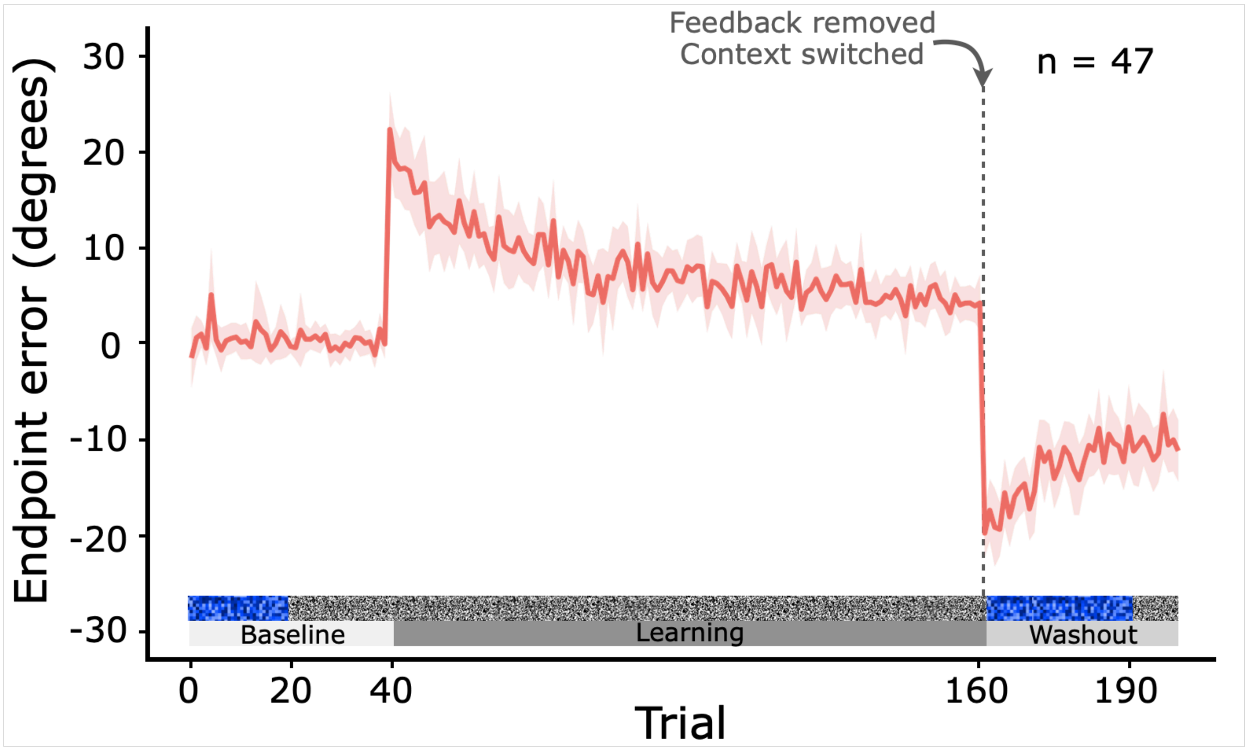

Fig. 4: Results of Experiment 3. In the Learning phase, participants adapted to a 30° rotation in a 'trained context'. After that, the context switched to the untrained one, and participants reached to the targets without visual feedback. Motor learning obtained in one context completely transferred to the other. The visual displays used for trained versus untrained contexts were counterbalanced across participants. The shaded area shows the 95% confidence intervals.

to associate them with outgoing motor commands. It is unclear which exact visual features are tracked by the adaptation system to compute SPEs. To begin to answer this question, we used novel visual displays across three VMR tasks, where participants could not rely on persistent features to track proxies of movement and compute SPEs. We found strong evidence for implicit adaptation even with such "featureless" objects, and adaptation was as (if not more) robust than in typical VMR tasks with discrete segmentable objects serving as visual feedback (Experiment 1a-b). This learning effect generalized to new movement directions in a canonical fashion (Experiment 2), and transferred completely from one context to the other (Experiment 3). These results clearly demonstrate that error-based implicit motor adaptation can occur without trackable, enduring visual properties from moment to moment, suggesting that higher-level visual information is used to compute SPEs during motor adaptation.

If persistent objects are not necessary in error-based visuomotor learning, what features about visual feedback are relevant? In our VMR tasks, the sensory output of a given hand movement is signaled by a sequence of random contrast changes propagating through space and time. Here, the motion is not signaled by persistent features or predictable local changes in luminance (i.e., first-order motion), but rather involves more complex cues that require higher-level processing in the visual system (i.e., so-called "second-order motion", [21, 22]). Second-order motion is thought to be processed by higher-level mechanisms in distinct areas of the visual system versus those involved in detecting first-order motion [23, 24]. These results, to our knowledge, are the first to demonstrate that second-order motion can induce equally robust implicit motor adaptation versus the first-order motion elicited by discrete segmentable objects, suggesting that sensory prediction errors depend on higher-level visual representations that require integration over larger spatial or temporal scales.

We note that our findings are consistent with a recent study by Warburton et al., who observed a nearly complete transfer of motor adaptation across two contexts defined by opposite directions of motion signals [12]. In their work, hand movement either translated a visible disc towards a target or caused the whole environment (the target and the background) to move to a static target. The transfer of learning they observed suggested that adaptation is not tied to the certain salient features of visual motion, like its direction. Relevant to the current study, the two contexts used by Warburton et al. still shared consistent visual features in common that can in theory be tracked to computing prediction errors (e.g., discrete segmentable objects moving in the scene). By using featureless-object displays, we found complete transfer of motor learning between two even more visually distinctive dynamic contexts that did not include segmentable objects, providing further evidence that prediction errors are computed without regard to basic visual features like motion energy or the movement of a segmentable objects.

Zooming out, we believe that our results pose a novel challenge to strict versions of the two-streams hypothesis, which proposes a dedicated visual pathway for visually-guided action that is largely independent from the pathway supporting perception. [25–27]. As has been shown in previous research [13], the visual system is capable of constructing perceptual representations of objects via unpredictable, "unsigned" changes that exhibit spatiotemporal correlations. Our findings build on this by demonstrating that the motor system is also able to use this type of abstract, higher-level visual signal to drive unconscious motor adaptation. This suggests that the boundary between perceptual and motor processing of visual information is less strict than often assumed. Future research may explore this question further by examining how different levels of visual representation can shape motor adaptation.

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