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RESEARCH ARTICLE

Control of Movement

Persistence of adaptation following visuomotor training

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Abstract

Retention tests conducted after sensorimotor adaptation frequently exhibit a rapid return to baseline performance once the altered sensory feedback is removed. This so-called washout of learning stands in contrast with other demonstrations of retention, such as savings on re-learning and anterograde interference effects of initial learning on new learning. In the present study, we tested the hypothesis that washout occurs when there is a detectable discrepancy in retention tests between visual information on the target position and somatosensory information on the position of the limb. Participants were tested following adaptation to gradually rotated visual feedback (15° or 30°). Two different types of targets were used for retention testing, a point target in which a perceptual mismatch is possible, and an arc-target that eliminated the mismatch. It was found that, except when point targets were used, retention test movements were stable throughout aftereffect trials, indicating little loss of information. Substantial washout was only observed in tests with a single point target, following adaptation to a large amplitude 30° rotation. In control studies designed to minimize the use of explicit strategies during learning, we observed similar patterns of decay when participants moved to point targets that suggests that the effects observed here relate primarily to implicit learning. The results suggest that washout in aftereffect trials following visuomotor adaptation is due to a detectable mismatch between vision and somatosensation. When the mismatch is removed experimentally, there is little evidence of loss of information.

NEW & NOTEWORTHY Aftereffects following sensorimotor adaptation are important because they bear on the understanding of the mechanisms that subserve forgetting. We present evidence that information loss previously reported during retention testing occurs only when there is a detectable discrepancy between vision and somatosensation and, if this mismatch is removed, the persistence of adaptation is observed. This suggests that washout during aftereffect trials is a consequence of the experimental design rather than a property of the memory system itself.

aftereffect; explicit strategy; implicit adaptation; visuomotor adaptation; washout

INTRODUCTION

Motor adaptation is characterized by a progressive behavioral change in response to systematic perturbations through an error-driven learning mechanism (1, 2). This behavioral change involves adjusting an already well-learned action to maintain performance levels by opting for an alternative well-practiced action or improving the current action. Movements in the absence of feedback following adaptation learning (aftereffect trials) enable the study of retention. Typically, in visuomotor adaptation paradigms, if a participant has learned to move leftward to counter a rightward rotation of visual feedback, removal of the feedback will result in the hand deviating toward the left as the participant tended to move leftward in anticipation of a rightward perturbation that is no longer there. Aftereffects are believed to be inherently transient. Indeed, adapted behavior rapidly regresses toward baseline values when altered feedback is removed (2–4). This phenomenon is commonly referred to as washout and occurs spontaneously. Kitago et al. (4) found that washout can have varied rates of decay that can be seen in different ways: switching off the perturbation, removal of relevant sensory feedback, using error clamp trials, and passage of time.

Although the reason for washout remains elusive, it is taken as evidence for the intrinsic decay hypothesis, the idea that sensorimotor memories established over the course of adaptation are subject to quick decay (5). The reversible nature of adaptation is in contrast to skill learning that

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normally occurs over long periods of time but tends to be durable. Nevertheless, some aftereffects of adaptation have been shown to persist over 24 h in visuomotor (6–8) and force-field (9, 10) learning. Furthermore, it has been shown that adapting to a perturbation that has already been learned previously (and apparently washed out) is usually faster than learning it for the first time (6, 8, 11, 12). This phenomenon is referred to as savings and suggests that the memory of the adapted state is not entirely eradicated. These contradictions have been addressed by Smith et al. (13) and Vaswani and Shadmehr (14), but cf. Refs. 12 and 15.

Tests for aftereffects are almost always conducted with an explicit visual target present. In a recent study, rather than using a single-point visual target in washout trials, Kumar et al. (7) tested for retention using a target arc that controlled for movement amplitude but provided participants with no directional information. Surprisingly, there was retention of learning and no evidence of washout either 5 min or 24 h after learning. Although the retention was incomplete at both time points, it was stable over repeated movements. In the present study, based on the results of Kumar et al. (7), we hypothesized that there is little loss of information over the course of aftereffect trials at the end of training. Rather, washout is due to a discrepancy between a seen visual target and the felt position of the limb. That is, washout occurs when visual information (target position in visuomotor adaptation paradigms) is provided and is incompatible with the felt position of the limb. Washout is absent when a detectable discrepancy between somatic and visual information is eliminated.

This hypothesis was tested using visuomotor adaptation tasks that were designed to engage either implicit learning mechanisms on their own or implicit and possibly explicit learning together. Our data indicate that if there is no discrepancy between somatic and visual information, or if the discrepancy is small enough to be minimally detectable, there is little loss of information in aftereffect trials. Washout occurs primarily following adaptation to large amplitude perturbations in which there is an easily detectable difference between the seen and felt position of the limb and, at that, only when visual information of target location is provided.

In control tests designed to eliminate the use of explicit strategies, patterns of decay were unaltered, which suggests that when washout is observed here it is primarily related to aspects of implicit learning.

MATERIALS AND METHODS

Participants

One hundred ten right-handed individuals with normal or corrected-to-normal vision (age 18–40 yr) participated in the study (10/condition). Participants were screened for mental-health and neurological disorders and were naive to the purpose of the experiment. The procedures were approved by McGill University Faculty of Medicine Institutional Review Board and participants provided written informed consent.

Experimental Setup

Participants held the handle of a two-degree-of-freedom robotic arm (InMotion2, Interactive Motion Technologies) and made reaching movements with the arm supported by an airsled. A Samsung monitor with a semi-silvered mirror was used to display the position of a cursor, target, and the movement start point. The mirror was placed just below eye level to block the vision of the participant's arm and the robot handle (Fig. 1*A*). Two 16-bit optical encoders (Gurley Precision Instruments) captured the real-time position of the robot arm over the course of the experiment. Headphones were used to signal the start of each trial and provide auditory feedback on movement duration or amplitude depending on the experiment (see *Detectable Visual Rotation* and *Visuomotor Adaptation*).

Experimental Environment

To minimize all but experimenter presented visual information from the experimental environment, the setup was covered by black cloth and the room was kept fully dark throughout the procedure. Thus, participants were unable to see and use edges or the workstation frame as a reference for their movements or their perceptual judgments. In all experiments, participants were instructed to make movements between 800 and 1,000 ms.

Detectable Visual Rotation

We conducted two preliminary studies to select a level of rotated visual feedback that limits participant awareness of the perturbation. In the first study, participants were asked to make outward reaching movements of 8 to 10 cm without a visual target. They were asked to alternately move between 30° to the left and 30° to the right relative to the body midline (Fig. 1*C*). Visual feedback of hand position was provided with a red cursor (7 mm diameter). Participants were told that on each trial, the visual cursor feedback would be rotated, either to the left or the right of their actual movement direction and their task was to indicate whether the rotation was rightward or leftward. No feedback on their judgments was provided. The start position for each movement was indicated with a gray circle (15 mm diameter) placed at 20 cm in front of the participants. On each trial, the visual cursor feedback was rotated by one of 11 values, five on each side of the hand movement direction (i.e., 5°, 10°, 15°, 20°, 25°) plus a zero-rotation condition. The instruction to alternate between movement directions was provided to minimize any use of strategies with the goal of ensuring that the participants' judgments were based only on the difference between the seen and felt direction of movement. On each trial, the start position turned green and an auditory cue was played to signal the start of the movement. Auditory feedback was provided at the end of each movement using a pure tone (low, medium, and high frequency) to inform participants of the amplitude of their movements. A movement that ended in the 8–10 cm range received a medium frequency tone. Movements that fell outside of this range received low and high-frequency tones, respectively. At the end of each trial, the robot brought the participants' arm back to the start position without visual feedback of its trajectory and held it there until the start of the next trial. No trials were discarded for being outside the 8–10 cm range. Each of the 11 possible rotations was repeated 15 times in a random order over the course of the experiment for a total of 165 trials.

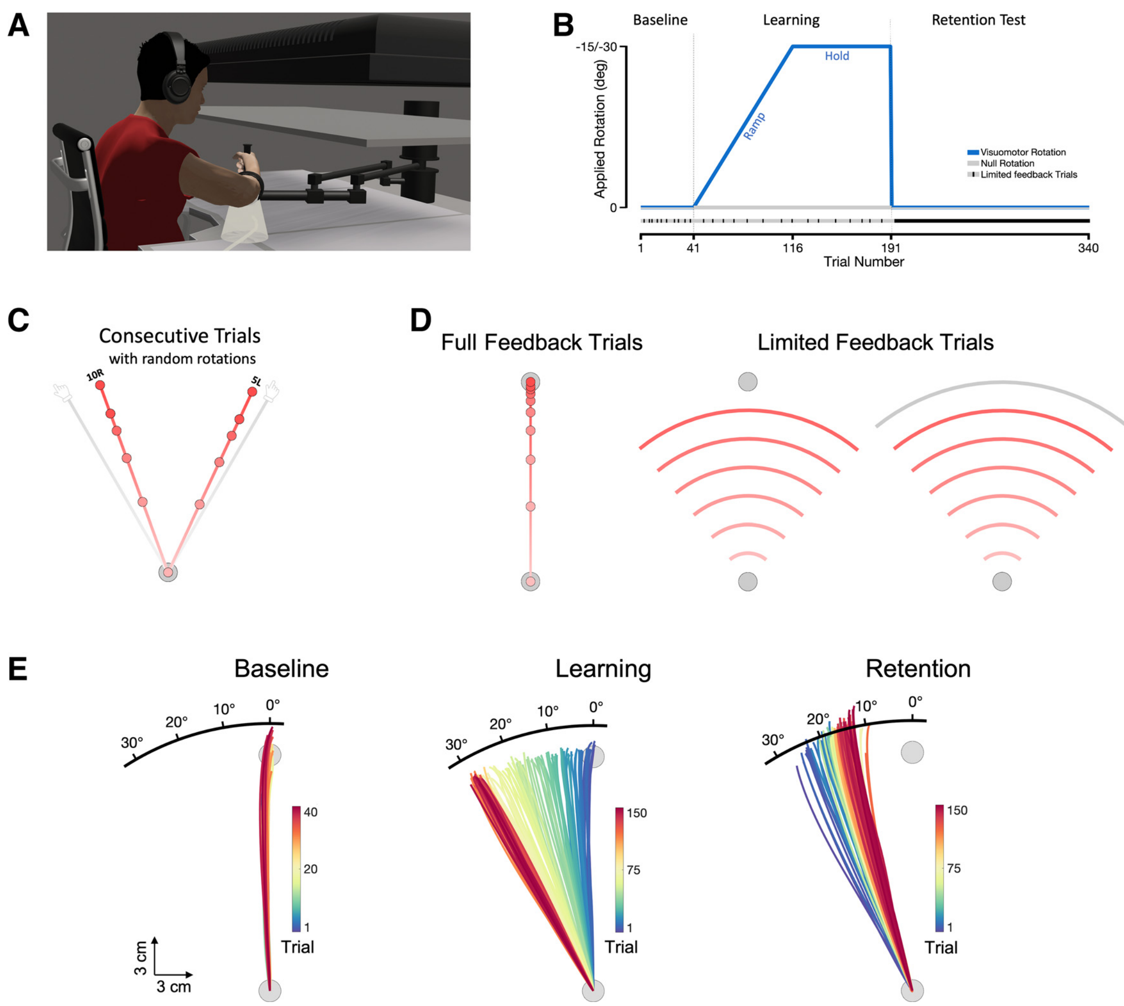

Figure 1. Participants were tested for retention of learning after a visuomotor adaptation task. *A*: experimental setup. Participants made standard point-to-point movements holding a robotic handle while an air sled supported their arm. *B*: after baseline trials, participants trained with either a null rotation (gray), or a gradually introduced visuomotor rotation (blue) with a 15° or 30° maximum value. A retention test was performed immediately after learning in which participants were asked to reproduce the movements they made at the end of training. Limited feedback trials are shown in black. *C*: participants alternately produced rightward and leftward movements in a perceptual judgment task, with random rotation magnitudes. Typical hand movement directions are shown in gray; examples of rotated visual feedback of different magnitudes are shown in red. *D*: in full feedback trials, a cursor showed real-time position of the participants' hand. Visual feedback of hand movement direction was gradually rotated in a clockwise direction over the course of training. Limited feedback trials were used for tests of retention. These trials were interspersed during baseline and learning; the only visual feedback was a growing semicircular arc. Depending on the experimental condition, the target in limited feedback trials could be either a circle or an arc. *E*: average hand paths during baseline, learning, and retention testing in the point target, 30° rotation condition (Point-30).

In a second study, a normal visuomotor rotation task was combined with explicit judgments about the direction of the applied rotation. As aforementioned, participants were instructed that visual feedback would be rotated on each trial and they were to indicate whether the rotation was to the right or the left. They were told nothing of the embedded adaptation task. Participants in this study were asked to make straight-ahead movements of 8–10 cm without any visual target. Visual feedback of hand position was provided by a red cursor (7 mm diameter). Participants were told that visual feedback would be rotated on each trial and their task was to indicate whether the rotation was to the right or the left. No feedback on their judgments was provided. The hidden adaptation task involved a familiarization phase of 25 movements, followed by a baseline phase of 30 additional trials. This in turn, was followed by movements with clockwise rotated visual feedback of hand position. This phase consisted of 160 trials in which the magnitude of the rotation was increased in steps of 0.2° on each trial, until on the 121st trial, the rotated feedback reached 20°. The magnitude of the rotated visual feedback was then held constant for a further 30 trials (Fig. 2*B*). To make participants believe that feedback was being consistently rotated in both directions (and not just clockwise), larger easily detectable rotations of 20° in both clockwise and counter-clockwise directions were introduced throughout the baseline and training phases. Hand direction, that is, the angle between the start position to the peak velocity point and a straight line corresponding to the body midline, served as a measure of learning in the adaptation trials.

The start position for each movement was indicated with a gray circle (15 mm diameter) placed at the body midline 20 cm in front of the participant. At the start of

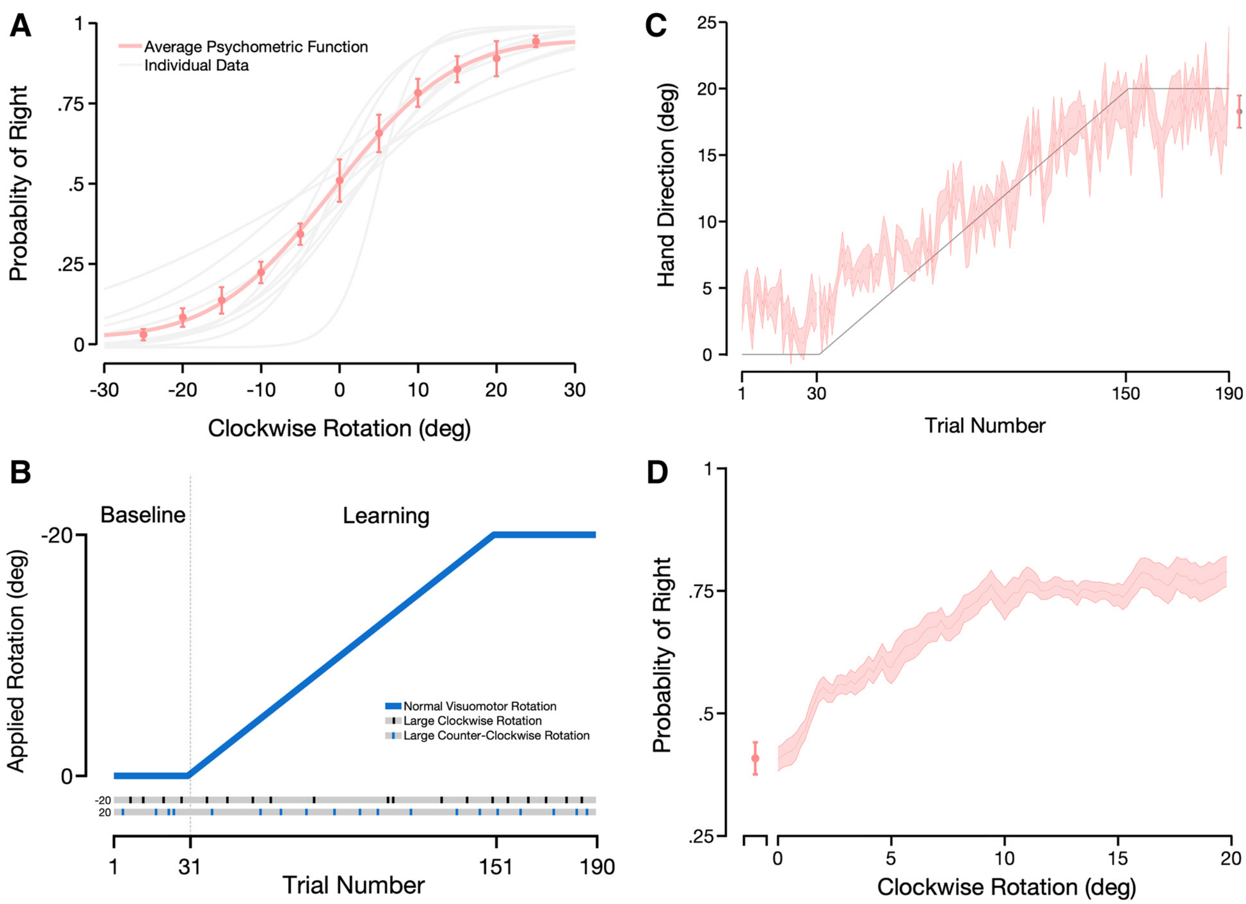

Figure 2. Rotation direction is not detectable until 10° and judgments remain at a threshold level of detection all the way up to 20°. *A*: a psychometric function was fit to the average proportion of "right" responses as a function of the rotation magnitude in degrees. Individual subjects are shown in gray. The threshold for detection of rotation direction is about 10° (75%). *B*: a visuomotor experiment combined with participants' rotation direction judgments was used to determine which rotations were detectable during training. After baseline trials, a gradually introduced 20° visuomotor rotation was concealed within rotation direction judgments. Large clockwise (blue ticks), and counter-clockwise (black ticks) rotations were interspersed. *C*: learning curves over the course of rotation direction judgments, showing mean hand direction at peak velocity across trials. Shaded areas represent the standard error of the mean. Solid lines in gray show the ideal hand direction that would fully compensate for the perturbation. *D*: the average proportion of "right" responses over a sliding window of 30 trials over the course of learning. Shaded areas represent the standard error. The error bar gives the average correct judgement level and standard error during baseline. Correct judgments during learning remain at a threshold level of detection right up to 20°.

each trial, the start point was shown with the cursor absent. The cursor was shown following a 1,000 ms delay and an auditory cue was played 500 ms later to signal the start of the movement. Once participants stopped moving, auditory feedback regarding movement distance was provided and afterward the robot brought the arm back to the start point without visual feedback and held it there in preparation for the next trial. No trials were discarded for being too long or too short.

Visuomotor Adaptation

Participants were asked to make point-to-point reaching movements from a start position to a target. The start position was a gray circle (15 mm diameter) placed at 20 cm in front of the participant at body midline; the target position was indicated with a second gray circle (15 mm diameter) 15 cm straight ahead of the start position. Real-time visual feedback of hand position was provided with a red cursor (7 mm diameter). At the start of each trial, the start and target points were shown with cursor absent. The cursor was shown following a 1,000 ms delay and an auditory cue was played 500 ms later to signal the start of the movement. After reaching the target, auditory feedback on movement duration was provided, relative to the desired 800–1,000 ms range. At the end of each trial, the robot brought the arm back to the start point without visual feedback and held it there until the next trial. As aforementioned, no trials were discarded for being too fast or too slow.

The adaptation task consisted of three consecutive phases. In a familiarization phase, participants made 25 movements with real-time visual feedback of hand position. This phase was followed by a baseline phase which consisted of 40 trials. Participants performed these movements as they did in the familiarization phase. The familiarization and baseline phases were interspersed with five and ten limited visual feedback trials, respectively. In these trials, the cursor was replaced with an expanding arc showing only the amplitude of movement. The target was replaced by a semi-circular target arc 15 cm from the start position. The required movement distance was the same in trials with a point target and with the semicircular arc (Fig. 1*D*). In the limited feedback trials, participants were instructed to move as before and to stop once the growing arc reached the target arc. In this way, no visual information was provided about movement direction while movement amplitude was controlled experimentally.

The baseline phase was followed by a training phase in which participants performed movements with clockwise rotated visual feedback of the hand position shown, as aforementioned, with a red cursor. This phase consisted of 150 trials. The magnitude of the rotation was increased in steps of 0°, 0.2°, or 0.4° (depending on experimental condition) on each trial, until on the 76th trial, the rotated feedback reached a predefined maximum rotation. The magnitude of the rotated visual feedback was then held constant for a further 75 trials (Fig. 1*B*). This gradual introduction of rotation was designed to minimize participant awareness of the perturbation. The maximum value of rotation was 0°, 15°, or 30°. See RESULTS and DISCUSSION for more information on selected rotation values. Fifteen limited visual feedback trials were interspersed within the training phase (eight during the ramp and seven during hold phase) as described earlier. The position of limited feedback trials was same for all participants. The hand direction served as a measure of learning. Participants were tested immediately afterward to assess retention (see *Retention Test following Visuomotor Adaptation*).

Retention Test following Visuomotor Adaptation

The training phase was followed immediately by a 150-trial test of retention during which participants were instructed to continue to make the movements they had been making in the training phase. All trials in this phase were performed with limited feedback, meaning that participants were only able to see the amplitude of their movements with a growing arc while the target could be either a point or an arc, depending on the experimental condition. Participants were instructed to stop once they reach the target. As in the learning task, the robot returned their arm to the start position once the movement was complete.

Experimental Conditions in the Visuomotor Adaptation Task

Participants were assigned to six different groups of ten individuals each. The groups were distinguished by the maximum visual feedback rotation value during training (0°, 15°, 30°) and the target type (point or arc) in the limited feedback trials. Participants in the *Arc-0*, *Arc-15*, and *Arc-30* conditions were presented with a target arc 15 cm away from the start point and underwent 0°, 15°, and 30° rotation during training. Similarly, participants in the *Point-0*, *Point-15*, and *Point-30* conditions were presented with a visual target point that was 15 cm from the start point and underwent 0°, 15°, and 30° rotation during training.

Kinematic Data Preprocessing

The hand position time series was sampled at 200 Hz. A zero-phase-lag second-order Butterworth filter was used to lowpass filter the data at a 10-Hz cut-off frequency. The position data were used to compute velocities. The change in hand movement angle across trials was used to quantify learning. The angle was calculated on each trial as the angle between a line connecting the start position to the target, and a line connecting the start position to the hand position at peak velocity.

Quantification

In the preliminary tasks, which assessed the perception of rotation direction, we asked participants to indicate whether visual feedback was rotated to the left or to the right of their own hand movement. A psychometric function was fit to the set of participants' binary responses at each angular deviation. To this end, for each participant, the proportion of "right" responses was calculated as a function of the rotation angle in degrees and a psychometric function was estimated using the average of proportions based on a cumulative Gaussian function (16). The goodness of fit (adjusted R^2) was computed between the average data points of individuals with those predicted by the psychometric function. Individual psychometric functions were estimated for all participants (Fig. 2*A*). In the second part of this study, which combined rotation direction judgments with a concealed adaptation task, the average percentage of correct rotation judgments ("right" responses) as a function of the angle of rotated feedback was calculated over a sliding window of 30 trials, over the course of adaptation training. The average of correct judgments in the baseline phase was also calculated.

In the main visuomotor adaptation task, the direction of hand movement at peak velocity was calculated relative to the straight line between the center of the start and target positions. To assess the retention of information during memory testing, the direction was computed both on a per trial basis and also averaged over the first two and last 40 trials of the retention test. Values were averaged across participants in each experimental condition to give estimates of the remembered direction. In addition to peak velocity, all results were also evaluated with hand direction at the end of movement. The time at which movement speed decreased to five percent of peak velocity was taken as movement end. To further asses the data pattern during the retention test, a linear, and an exponential equation in the form of $a^{*}\exp\left(-\frac{x}{\tau}\right) + c$ were fit to each individual's data, where a refers to the amplitude, τ to the time constant, and c to an offset. The fits were computed using a Levenberg–Marquardt least-squares optimization algorithm. No restrictions were imposed on the coefficients. The Bayesian information criterion (BIC) was used to select the best fit between the linear and exponential models for each individual (17, 18). The initial and final estimated data point of each participant were extracted from their associated model to calculate the amount of decay predicted over the 150 aftereffect trials using the following formula: $(\theta_i - \theta_f)/\theta_i$ in which θ refers to participants' remembered direction estimated by their associated best fit model, with subscripts i and f referring to the initial and final values, respectively (see Fig. 5*B*).

Statistical Analysis

Analysis of variance (ANOVA) was used to compare retention values in the different experimental conditions, taking data from the beginning and the end of the retention test.

The same analysis was used to assess learning at the end of visuomotor training relative to baseline performance. The rotation magnitude (0, 15, 30) and target type (point, arc) were treated as between-subject factors and the time within the experimental sequence (beginning and end of either learning or memory test) as a within-subjects factor. Hand direction at peak velocity, in degrees, served as a dependent measure. In retention tests, movement direction was calculated as the average of the first two (beginning) and last 40 trials (end). The first two trials alone were used to minimize possible transient changes in the value of this measure due to washout at the beginning of the retention test. In assessments of learning, hand direction was averaged over baseline trials and over the last 70 trials of the learning phase.

RESULTS

We ran a perceptual judgment task to find a level of rotated visual feedback that limits participant awareness of the perturbation and then used this threshold value in a second experiment to engage implicit learning mechanisms. In the perceptual task, participants held a robot handle and made outward movements without visual targets (Fig. 1*A*). They were asked to alternate on consecutive trials between 30° to the left and 30° to the right relative to their body midline. Participants were told that on each trial visual cursor feedback would be randomly rotated to the left or to the right of their hand movement direction (Fig. 1*C*) and their task was to indicate whether this rotation was leftward or rightward. A psychometric function was fit to the average of the rightward responses across participants as a function of the rotation magnitude in degrees (Fig. 2*A*). The adjusted R^2 (goodness-of-fit) was equal to 0.99. It can be seen that the threshold for detection of rotation direction is ~10° and that judgments are not consistently accurate even at 20° (the 75th percentile of the psychometric function is taken as the detection threshold in a two-alternative forced choice task).

A second study focused on establishing a level of rotated visual feedback that was not detectable during learning. For this purpose, we embedded a visuomotor rotation manipulation within a task involving judgments of rotation direction. Subjects were led to believe that they were doing a perceptual judgment task, as aforementioned, and were told nothing of the gradually rotated visual feedback. Large amplitude, easily detectable, rotations in both directions were interspersed on 20% of trials to make subjects believe that feedback was being consistently rotated in both directions. The rotation angle was clamped to 20° in these trials. The task was performed without any target at all. Participants were asked to move their hand straight out on the body midline and to judge, whether, based on cursor feedback, the applied rotation was to the left or to the right of their hand movement direction.

Figure 2*B* shows a summary of the different phases of this experiment, with the placement of the large amplitude rotations shown at the bottom. The baseline movements were done without rotated feedback, followed by a block in which visual feedback was gradually rotated, up to 20° clockwise, and then held constant. Figure 2*D* shows the percentage of correct judgments as a function of the angle of rotated feedback (with the larger rotations removed). In this figure, each data point was calculated using the average proportion of "right" responses over a sliding window of 30 trials, starting at the training block. The correct judgment average in the baseline phase is also included. It can be seen that the accuracy of rotation direction judgments is no better than chance until around 10° and that correct judgments of rotation direction remain at threshold levels of detection (75%) right up to 20°. Nevertheless, Fig. 2*C* shows that participants do adapt to these perturbations ($t_{(9)}$ = 12.38, $P < 0.001$). Based on the results of both of the aforementioned studies, we used gradually introduced 15° visual feedback rotations in subsequent experiments, to engage implicit learning mechanisms in assessments of adaptation and retention. Gradually introduced 30° rotations, which are consistently detectable (Fig. 2*A*), were used to engage both implicit and possibly explicit mechanisms as well.

The primary study in this paper focused on the retention of learning. Participants held a robot handle (Fig. 1*A*) and made reaching movements with either full visual feedback or limited visual feedback (Fig. 1*D*). In full feedback trials, hand position was indicated with a cursor; in limited feedback trials, the cursor was replaced by an expanding arc that provided information on movement amplitude but not direction. Participants made baseline movements without rotated feedback followed by a learning phase, in which visual feedback was rotated gradually over 75 trials to 15° or 30° clockwise and was then held constant for a further 75 trials. After the visuomotor adaptation task, participants were immediately tested for retention. In the retention tests, participants were asked to reproduce the movements which they performed at the end of learning. In this phase, the visual feedback of hand position was removed and replaced with an expanding arc (Fig. 1*D*, right side). A summary of the different phases of the experiment is shown in Fig. 1*B*.

Figure 1*E* illustrates the average hand trajectories in different phases of the experiment for participants who learned a 30° clockwise visuomotor rotation with the target present throughout the experiment. It is seen that over the course of the training block, participants showed adaptation to the visual perturbation. Hand trajectories in this phase progressively shifted in a direction opposite to the perturbation, which compensated for the imposed rotation (Fig. 1*E*, *middle*), and as a result, the cursor moved roughly straight toward the target throughout the learning phase. As this figure shows, participants maintained the learned hand direction throughout the hold phase. During the retention test, hand direction rotated back in a clockwise direction, reaching a final angle of ~15°.

Figure 3 shows hand movement direction over the course of learning for trials in which participants received cursor feedback (Fig. 3*A*) and trials with limited feedback in which they received amplitude but not movement direction information (Fig. 3*B*). It can be seen that in both the 15° and 30° conditions participants adapt fully to the imposed perturbations. Movements during limited feedback trials resemble those with full visual feedback. Learning was assessed statistically by comparing performance in baseline trials with those at the end of training. Supplemental Fig. S1 (all Supplemental Figures are available at https://doi.org/10.6084/m9.figshare.21222092) shows quite similar results when the hand angles at the end of movement replaced those at peak velocity.

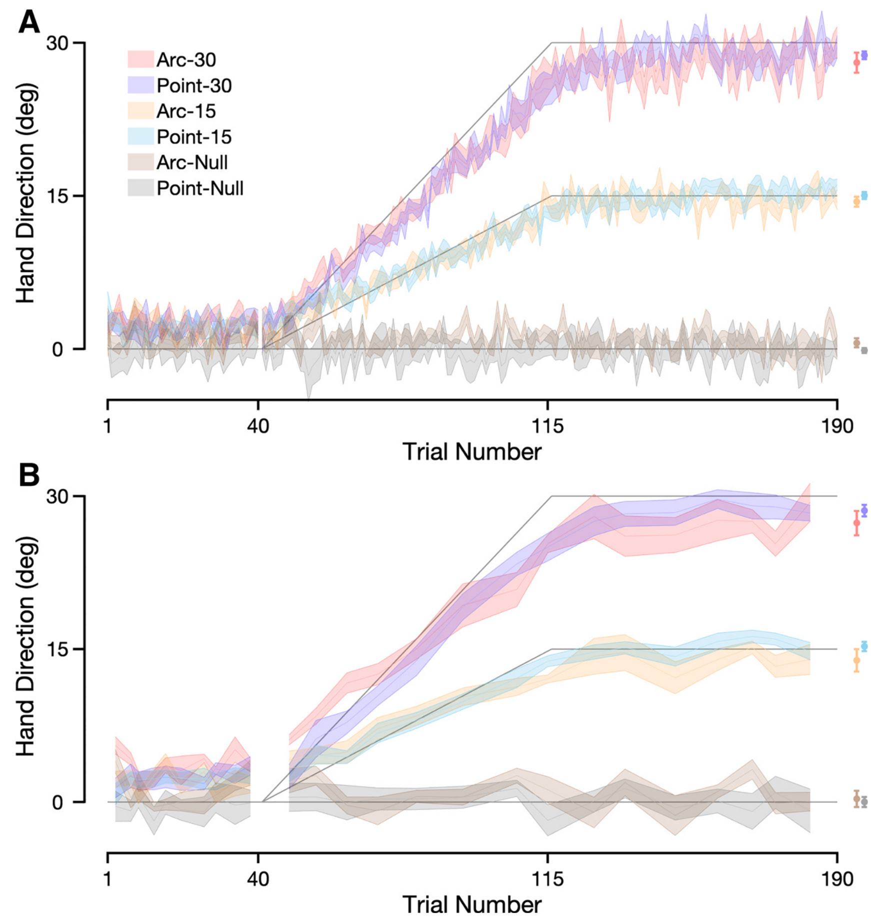

Figure 3. Participants compensated for the imposed visual perturbation during learning. Movement direction was maintained in limited feedback trials. Hand direction in null rotation conditions was close to zero. *A*: learning curves showing mean hand direction at peak velocity across subjects. Shaded areas give the standard error. Solid lines in gray show the hand direction that would fully compensate for the perturbation. *B*: mean hand direction at peak velocity during limited feedback trials. Dots and error bars represent the mean and standard error of hand direction for the last 70 trials in *A*, and last 7 limited feedback trials in *B*.

Statistical tests were conducted for full visual feedback and limited feedback separately. When subjects trained with full feedback, there were different amounts of adaptation for the different rotation levels. Specifically, there were no differences in performance in baseline trials. At the end of training, hand movement direction differed depending on the magnitude of the rotated feedback ($F_{2,54}$ = 353.43, $P <$ 0.001, ω^2 = 0.810). For each rotation angle (0, 15, 30) there were no differences in performance between the movement to point versus arc targets ($F_{1,54}$ = 0.04, P = 0.834). For participants that trained under null rotation conditions, there were no differences between baseline values and performance measured at the end of training ($F_{1,54}$ = 0.73, P = 0.433).

Similar results were obtained for trials involving limited feedback. Specifically, performance differed at the end of training depending on the rotation angle ($F_{2,54}$ = 296.68, $P <$ 0.001, ω^2 = 0.782). Arc and point targets produced similar performance ($F_{1,54}$ = 2.08, P = 0.199). No changes in performance levels were observed for participants that trained with null rotation ($F_{1,54}$ = 0.16, P = 0.690).

Immediately after the visuomotor training, memory for the learned movements was tested by having participants move either to a point target or to a target arc. In each case, feedback during movement was limited to an expanding arc that provided amplitude information alone. The average hand direction during the retention tests is shown in Fig. 4*A*. It can be seen, with two exceptions, that participants moved almost in the same direction that they trained in during the learning block. Little loss of information is evident. When retention testing is conducted with a visual target present, there is washout, that is, a progressive loss of information that approaches an asymptotic value of ~15° for the *Point-30* and a value of ~12° for the *Point-15* condition. It can also be seen that participants who trained with null rotations show movement angles near to zero degrees (straight ahead) during the retention tests which indicates that the retention testing procedure does not bias the outcome. The same results were obtained when the hand angles at the end of the movement were used instead of at peak velocity, as shown in Supplemental Fig. S2.

We first evaluated differences in performance between the end of training and the initial retention test trials that were conducted with limited visual feedback. It was found that although mean differences were small (30° vs. 28°; 15° vs. 13°), hand movement angles at the beginning of the retention test were reliably less than those at the end of training ($F_{1,54}$ = 7.45, P = 0.009, ω^2 = 0.032). Participants who trained in the null condition had hand angles during the retention test that were not different than zero (t_{19} = 1.03, P = 0.316).

ANOVA was conducted to assess differences in movement direction during the retention test. To this end, the average of hand angles over the first two, and last 40 trials of the test were used. Overall, there was a reliable difference in movement direction for the three different training conditions ($F_{2,54}$ = 314.27, $P <$ 0.001, ω^2 = 0.792). No overall reliable difference was found between movements to point and arc

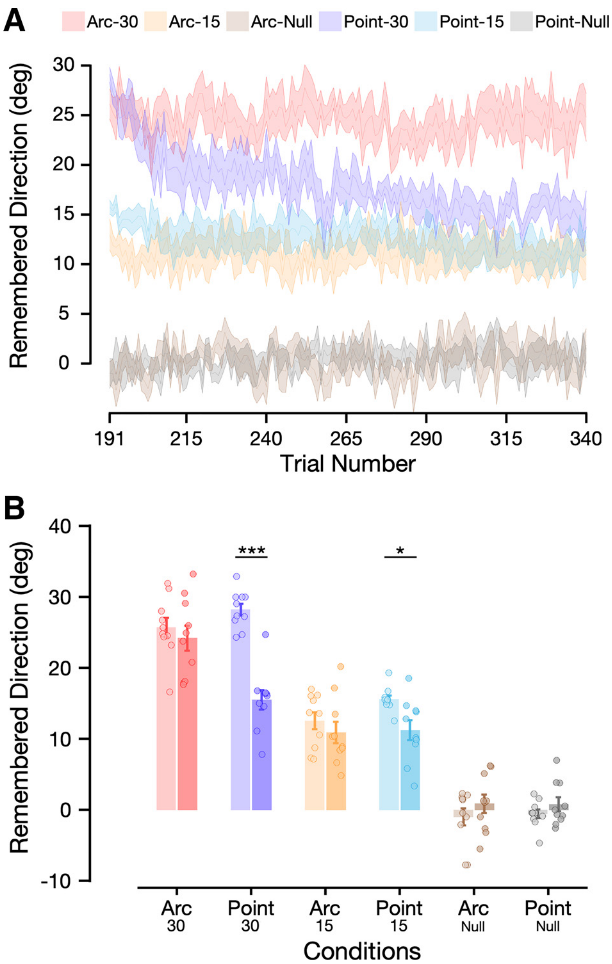

Figure 4. Washout in retention tests following learning is observed only when a visual target point is shown. Participants in null rotation conditions showed hand directions close to zero. *A*: mean hand direction during retention tests. Except for the Point-30 and the Point-15 conditions, movement direction remained stable throughout the retention test and close to the value needed to compensate fully for the original perturbation. *B*: mean remembered direction over the first two (light colors) and last 40 (dark colors) trials in *A*. There was a significant difference in the remembered direction between the beginning and the end performance of participants in the Point-30 and the Point-15 conditions. Dots and error bars represent single subjects and standard error, respectively. Point and Arc refer to the type of visual target during retention testing. 0, 15, and 30 indicate the visual feedback rotation magnitude during training. Reliable differences are indicated with *$P < 0.05$ and with ***$P < 0.001$.

targets ($F_{1,54}$ = 0.28, P = 0.60). The key analysis was an assessment of differences in hand angle between the start and end of the retention test, corrected for multiple comparisons. As can be seen in Fig. 4*B*, we observed a reliable difference in hand angle between the start and end of the retention tests, when a point target was used in retention test trials, after training both with 30° ($F_{1,54}$ = 804.73, P < 0.001) and 15° rotated feedback ($F_{1,54}$ = 7.22, P = 0.025). No other reliable differences were obtained between the start and end of the retention tests.

To assess the loss of information during the retention test, a linear and an exponential function was fit to each participant's data and the best fit was selected between them based on the Bayesian information criterion (BIC). A quantitative evaluation of normalized decay in different experimental conditions is presented in Fig. 5*B* (see MATERIALS AND METHODS). ANOVA indicated an overall reliable difference in the normalized decay rate between movements to the point and arc targets ($F_{1,36}$ = 21.84, P < 0.001, ω^2 = 0.348). Null conditions were discarded from this analysis. No overall reliable difference was found between training at 30° and 15° ($F_{1,36}$ = 1.11, P = 0.299). Similar results were obtained when only exponential and only linear fits were used. For the individual fits, BIC indicated that a linear model best described the data for all participants in the *Arc-30*, three participants in the *Point-30*, and seven participants in each of the other conditions. For visualization purposes, we have included in Fig. 5*A* the average data in each of the conditions and the best overall fit, also based on BIC.

Finally, two control studies were conducted. One evaluated the possibility that the stability of motor memory in the *Arc-30* and *Arc-15* conditions was a result of a context change from the training phase to aftereffect trials, in which

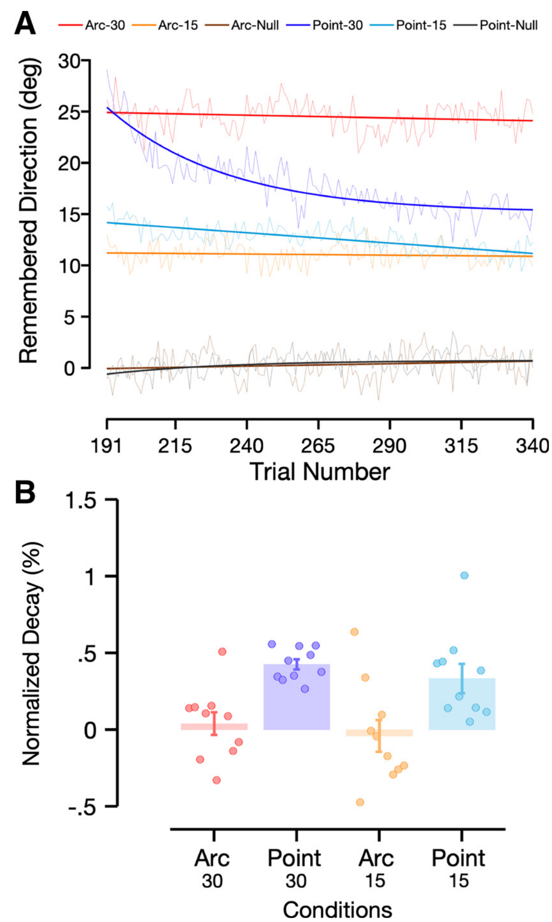

Figure 5. *A*: for visualization purposes, the best overall model, based on Bayesian information criterion (BIC), was fit to the averaged data in each of the experimental conditions. The models predict a transient change in movement direction during the retention test in the Point-30 and Point-15 conditions. *B*: normalized decay was calculated using the first and final data point of the best fit for each participant (Null conditions were discarded). Point and Arc indicate target type during the retention test; 30 and 15 are the visual feedback rotation magnitudes during training. ANOVA indicated an overall difference between movements to the point and arc targets when normalized decay served as the dependent variable.

the target point was replaced with target arc. A second assessed whether the performance of participants during aftereffect trials changed when given instructions in this phase which minimize the possible use of explicit strategies.

In the first control study, a new experimental condition, *PointArc-30*, was tested in which a target point was shown on top of the target arc during the aftereffect trials. The training phase was identical to that in the main visuomotor adaptation task. In this way, there was a context change from the training phase to the aftereffect trials, however the exact position of target was shown. If the absence of washout seen earlier in Fig. 4*A*, was due to a context shift between training and test phases, retention of learning might likewise be expected here. On the other hand, if washout is due to the presence of the point target and associated visuo-somatic mismatch, then it should be expected here as well, in spite of the context shift. The results of the control study suggest the latter is correct. Figure 6*A* compares the average hand direction at peak velocity of participants during retention test in *PointArc-30* and *Point-30* conditions. It can be seen that the start point, asymptote and the rate of decay for both conditions are similar. ANOVA indicated no overall difference between these conditions ($F_{1,18}$ = 0.1, P = 0.757). However, as expected, there was an overall reliable difference between the hand direction at the start and end of the retention test ($F_{1,18}$ = 82.09, $P < 0.001$, ω^2 = 0.575). A simple main effects analysis showed hand direction at the end of the retention test was less than at the beginning for both *Point-30* ($F_{1,18}$ = 101.92, $P < 0.001$) and *PointArc-30* ($F_{1,18}$ = 24.54, $P < 0.001$) as shown in Fig. 6*B*. Similar results were obtained when hand direction at the end of movement was used instead of peak velocity.

In the second control study, the *Point-30* and *Point-15* conditions of the main visuomotor adaptation task were repeated with a change in instructions designed to minimize the contribution of explicit aiming strategies. This time instead of instructing participants to "continue to make movements that you have been making in the training phase," participants were told "stop using any strategy you might have been using and move straight to the target." These two new conditions are called *Point-30*(SR) and *Point-15*(SR). Figure 7*A* compares the new conditions with those of the main visuomotor adaptation task, using hand direction at peak velocity as the dependent variable. ANOVA confirmed there was no overall reliable difference between hand direction when the instruction for the aftereffect trials was changed ($F_{1,36}$ = 0.02, P = 0.887). There was an overall reliable difference between the 15° and the 30° condition ($F_{1,36}$ = 125.51, $P < 0.001$, ω^2 = 0.627) as well as for the hand direction at the start relative to the end of the retention test ($F_{1,36}$ = 145.36, $P < 0.001$, ω^2 = 0.635). Simple main effects analyses indicated there were reliable differences between the start and the end of retention test in *Point-30* ($F_{1,36}$ = 101.92, $P < 0.001$), *Point-30*(SR) ($F_{1,36}$ = 68.95, $P < 0.001$), *Point-15* ($F_{1,36}$ = 7.22, P = 0.025), and *Point-15*(SR) ($F_{1,36}$ = 10.18, P = 0.011) as shown in Fig. 7*B*. Using hand direction at the end of movement led to similar results.

DISCUSSION

The goal of this study was to determine whether there is the persistence of adaptation following visuomotor training, and, in cases where washout is observed in aftereffect trials, to establish the reason. We hypothesized that information loss during retention testing occurs only when there is a detectable discrepancy between vision and somatosensation. We tested this idea by constructing a retention test with two different target types, one that led to this discrepancy and the other, which did not. Specifically, when the retention test involved movements to a point target there was a mismatch between the seen target location and the felt position of the limb. An arc target produced no such discrepancy because the only directional information available during movement was somatic.

Retention tests showed that much of the initial learning was retained over the course of aftereffect trials. Estimates of the remembered direction at the beginning of the memory test were similar to what participants learned over the course

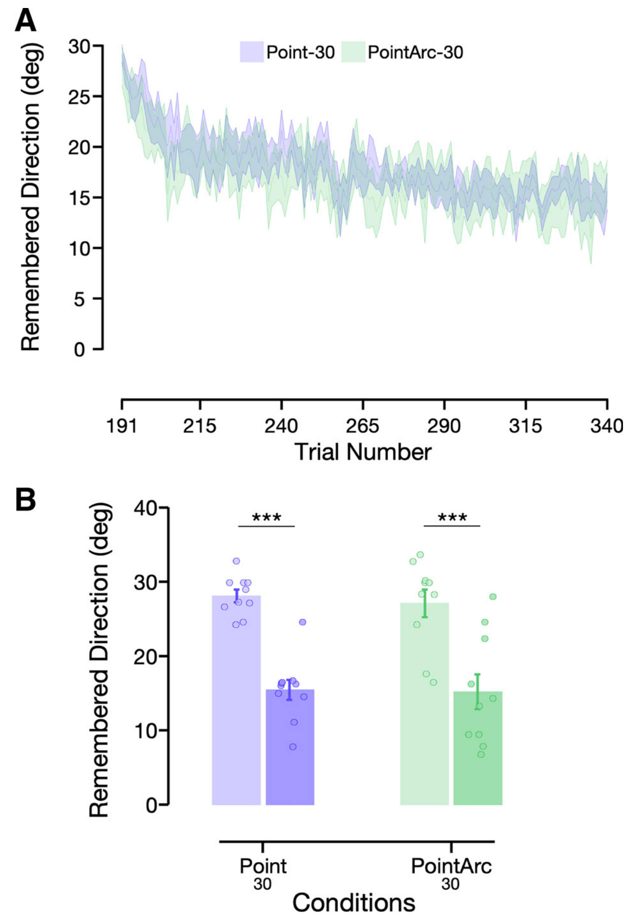

Figure 6. Retention of learning is not due to a context shift between training and aftereffect trials. Washout is dependent on the presence of a point target along with a visuo-somatic mismatch of a detectable magnitude. *A*: in the *PointArc-30* condition, a target point was shown on top of the target arc; the training phase was identical to the Point-30 condition in the main visuomotor adaptation task. The hand direction pattern over the course of the retention test was similar in *Point-30* and *PointArc-30* conditions. *B*: mean remembered direction at peak velocity over the first two (light colors) and last 40 (dark colors) trials in *A*. Although no overall differences were found between *Point-30* and *PointArc-30* conditions, there was, as expected, a reliable overall difference in performance between the start and the end of the retention test. Point and PointArc indicate the target type during the retention test; 30 refers to the visual feedback rotation magnitude during the training phase. Reliable differences are shown with $^{***}P < 0.001$.

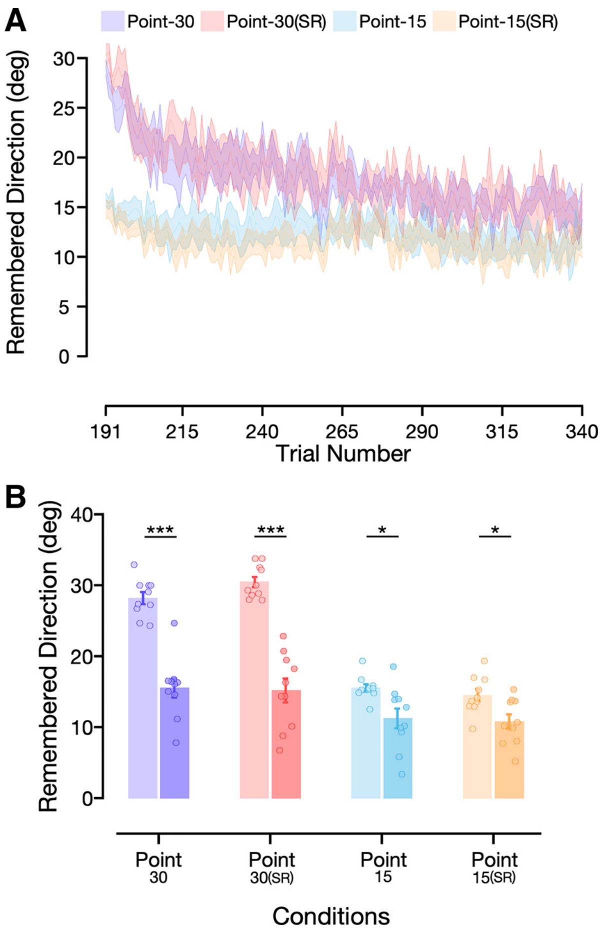

Figure 7. There was no difference in performance when participants where participants were instructed to minimize any possible use of an aiming strategy during the retention test. *A*: although participants in *Point-30*(SR) and *Point-15*(SR) conditions were told to stop use any strategies they might have been using and point straight to the target, the data in these conditions are similar to that of the *Point-30* and *Point-15* conditions of the main visuomotor adaptation task, suggesting that washout was not due to an explicit aiming strategy. *B*: mean remembered direction at peak velocity over the first two (light colors) and last 40 (dark colors) trials in *A*. There was no overall reliable difference in performance when the instructions during the retention test were changed. However, there was an overall reliable difference between the 30° and 15° conditions. The remembered direction at the start and end of the aftereffect trials also differed. Point refers to the type of visual target during the retention test; 30 and 15 are the visual feedback rotation magnitudes during training. Reliable differences are indicated with $*P < 0.05$ and with $***P < 0.001$.

of training, although a statistical analysis showed a small difference in favor of initial learning. The movement pattern was shown to be stable, except when retention tests were conducted using a point target, following training with a 30° visuomotor rotation and to a lesser extent following training with a 15° rotation (Fig. 4*A*). In these latter cases, the position of the target was visible and did not match the position of the limb.

The present study shows that there is persistence of adaptation following learning in the absence of a visuo-somatic mismatch. Washout, when present, appears to be a property of the experimental procedure that occurs when there is visuo-somatosensory mismatch that is of a detectable magnitude, and not a property of the memory system itself. Washout is not an indication that adaptation learning is inherently unstable. On the contrary, the present study, in combination with earlier work using both active movement and recognition tests of prior visuomotor learning (7) indicate that adaptation learning is durable. It decreases slightly following learning and again overnight, but it is then stable for up to 24 h. Moreover, as shown here, the basic patterns are similar following adaptation to small and large amplitude perturbations, which speaks to the generality of the observed persistence.

The use of small and large amplitude rotations enabled us to identify two parts to visuomotor adaptation, one which is almost wholly subconscious and a second which is large enough to be detectable and subject to washout when there is a visuo-somatic mismatch. Evidence for the former, which is engaged in compensating for small amplitude rotations, is that even when participants were explicitly required to indicate the rotation direction, their performance was no better than threshold levels of accuracy, but they nevertheless adapted to the rotated feedback. The adaptation that occurs under these conditions remains stable over time. Even when there is a visual somatic discrepancy in the retention test trials (as with a point target following training with a 15° rotation), when the mismatch is of a magnitude that is not easily detectable (as seen in Fig. 2), little loss in information is evident in aftereffect trials. With larger perturbations, such that the visuo-somatic mismatch is in the detectable range, washout occurs, and this part of the learning appears to be labile. This component to learning seems to be implicit in the sense that it is present following manipulations aimed at minimizing explicit strategies such as aiming. This second part to adaptation, thus appears to occupy a middle ground between wholly implicit, subconscious learning and cognitive factors such as re-aiming. The change in visuo-somatic mapping is large enough to be detectable, rendering the adaptation labile during aftereffect testing. Yet it is seemingly minimally cognitive or explicit in the sense of providing an intentional contribution to performance.

We conducted a control study to assess the possibility that the absence of washout with an arc target might be due to a context change between training movements to a point target and aftereffect movements to an arc, rather than to persistence of learning per se The control study also involved a context shift but one in which the target for washout trials was an arc with a point target superimposed. If the retention observed previously with an arc target was due to a context shift, we would expect to see the same pattern of retention in the control study. Instead, we found that as long as a point target is present (even superimposed on the target arc), then normal patterns of washout are observed. This indicates that the absence of washout seen with an arc target is not because of a context shift but because it eliminates a visuo-proprioceptive mismatch that occurs when a target is present.

The present results are consistent with previous reports of washout, which is observed when adaptation to large amplitude perturbations is followed by retention tests with explicit visual targets (2, 4, 11, 19, 20). The factor that distinguishes this particular condition (30° rotation, point target) from the remainder of the conditions tested in the present studies is the large and presumably readily detectable mismatch between the position of the visual target and the arm. The aftereffect trials put vision and somatosensation in conflict, and as has been observed elsewhere, under these conditions vision wins (21); movement patterns change to reduce the discrepancy between the visual target and felt position of the limb.

The persistence of motor memory has been shown in prior studies that have focused on interference effects following learning and separately on motor memory retrieval failure. Persistence is seen when there are multiple competing motor memories. An example of this is when people learn two opposite perturbations successively (6, 22, 23). It is found that the initial learning interferes with the learning which follows; shorter intervals following the initial learning phase yield increased interfering effects. In other work, motor memory retrieval is impeded by the prior retrieval of other items (24, 25).

To differentiate possible contributions to washout, we conducted a number of control studies to establish the point at which participants were capable of detecting visuo-somatosensory discrepancies. We reasoned that any adaptation that occurred in conjunction with nondetectable differences would be reliant on wholly implicit learning mechanisms. To this end, two different experiments were conducted to identify levels of visuomotor rotation that were small enough to go undetectable. In the first, participants were informed that as they made movements the visual feedback of their hand position would be rotated and that they were to judge whether the visual displacement was to the right or the left of their own movement. This experiment showed that judgments were at chance below 10° and not entirely accurate even at 20° (Fig. 2*A*). In a second study, to assess to point at which gradually introduced rotations of visual feedback might be detectable during learning, we combined a standard visuomotor adaptation task with judgments of rotation direction. As in the previous experiment, participants were told that visual feedback would be rotated on each trial, and that following each movement they were to indicate whether the rotation was to the right or left. They were told nothing of the embedded adaptation task. This procedure produced normal visuomotor adaptation, however, as in the first experiment, rotation direction judgments were at chance level until 10° and remained at threshold levels of detection (75%) all the way up to 20°.

The present results are in line with previous work on implicit visuomotor adaptation. Implicit learning in the range of 10° is observed in no feedback trials following learning (26, 27); 20° appears to be an upper bound on implicit learning, based on work using visual error clamps (11, 28, 29). It has been shown that 30° of rotation is large enough to engage explicit aiming in adaptation (11, 30–33), although our control tests suggest that in the present study, learning with both 15° and 30° visuomotor rotations is restricted to implicit mechanisms. As in the present studies, work showing decay of implicit learning has been previously reported (26, 27, 31, 33). However, in other work, it has been proposed that given a sufficient amount of training, implicit adaptation would compensate for the majority of sensorimotor discrepancies even if there are very large errors (5, 34, 35).

It should be noted that the visuo-somatic mismatch in the detection experiments in the present studies is different from that involved in learning. In the detection experiments, there is dynamic mismatch between vision and proprioception throughout whereas during washout trials the visual target is stationary while the limb moves outward. There is indirect evidence that the two situations are functionally equivalent as estimates obtained with the two different procedures converge on the same value. That is, retention trials with a point target asymptote at the same value as that identified under conditions of dynamic mismatch.

We have argued that washout following visuo-motor adaptation is attributable to a detectable mismatch between a visual target and the felt position of the limb. Other potential interpretations are worth considering. Point and arc targets may differ in tolerance for the accuracy of the reaching movement or possibly because the two conditions differ in terms of a higher-level goal. These differences in strategy rather than retention of information per se may account for the apparent stability in the arc target condition. A further possibility is that a difference in context between training and retention trials may be the source of persistence. A control study was conducted to assess this possibility, however, the shift in context in the control study nevertheless included a point target that raises the possibility that the context shift was incomplete, and hence washout was observed as a consequence. One way to directly test the idea that washout is due to a visuo-proprioceptive mismatch would be to explicitly manipulate the degree of the mismatch. This might be done, for example, by replacing visual targets during washout trials with clamped visual feedback of movement direction. The clamped feedback could either correspond to a displacement directly toward the previous target location, which would result in a mismatch, or alternatively, visual feedback could be clamped to the actual direction of movement, which would eliminate the mismatch. Participants would be instructed to point directly to the previous target location and to ignore the visual feedback. If washout is due to a discrepancy between visual and somatic information, it should be seen only in the case where clamped visual feedback and limb movement direction differ.

In summary, motor memory retention was tested following visuomotor adaptation. The findings show that motor memory is persistent following learning. Washout occurs only when feedback rotation is large enough to be detectable and when a target point is used, providing a discrepancy between human vision and somatosensation. Aftereffect trials using a target arc removed this discrepancy such that the remembered direction remained stable during the test of retention. Regardless of target type, when corrections were at levels that were not detectable washout was limited at best.

SUPPLEMENTAL DATA

Supplemental Figs. S1 and S2: https://doi.org/10.6084/m9.figshare.21222092.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

S.E. and D.J.O. conceived and designed research; S.E. performed experiments; S.E. analyzed data; S.E. and D.J.O. interpreted results of experiments; S.E. prepared figures; S.E. and D.J.O. drafted manuscript; S.E. and D.J.O. edited and revised manuscript; S.E. and D.J.O. approved final version of manuscript.

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