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Decomposition of a Sensory Prediction Error Signal for Visuomotor Adaptation

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To accomplish effective motor control, the brain contains an internal forward model that predicts the expected sensory consequence of a motor command. When this prediction is inaccurate, a sensory prediction error is produced which adapts the forward model to make more accurate predictions of future movements. Other types of errors, such as task performance errors or reward, play less of a role in adapting a forward model. This raises the following question: What unique information is conveyed by the sensory prediction error that results in forward model adaptation? sensory prediction errors typically contain both the magnitude and direction of the error, but it is unclear if both components are necessary for adaptation or a single component is sufficient. In this article, we address this by having participants learn to counter a visuomotor rotation, which induces an angular mismatch between movements of the hand and visual feedback. We manipulated the information content of the visual feedback, in the form of a line, which accurately represented only the magnitude (distance), direction, or both magnitude and direction, of the virtual cursor relative to the target. We demonstrate that sensorimotor adaptation does not occur, or is minimal, when feedback is limited to information about the magnitude of an error. In contrast, sensorimotor adaptation is present when feedback is limited only to the direction of an error or when it contains combined direction and magnitude information. This result stands in contrast to current computational models of cerebellar-based sensorimotor adaptation that use error magnitude to drive adaptation.

Public Significance Statement

When movements are errant, a sensory prediction error—signaling the difference between expected and actual consequences of a movement—is thought to update this prediction for future movements, which is a process known as *sensorimotor adaptation*. We decomposed an error signal during a visuomotor rotation task into its constituent parts (i.e., direction and magnitude) to investigate which components of an error signal give rise to adaptation. True adaptation, as measured by the presence of an aftereffect, only occurred when feedback contained direction information. This form of adaptation was minimal when feedback only contained magnitude information. These results present a challenge to current models of sensorimotor adaptation that use error magnitude to drive learning, and complicate the understanding of the neural mechanisms involved in sensorimotor adaptation.

Keywords: sensorimotor adaptation, motor learning, error decomposition, sensory prediction error, explicit learning

Visuomotor adaptation is fundamental for maintaining accurate control of movement (Cunningham, 1989; Krakauer et al., 1999). To gain insight into this process, studies often induce a mismatch between the desired action and the resultant feedback using prismatic distortions (Welch, 1978 and 1986) or visuomotor rotations (for a review, see Krakauer, 2009). Typically, at the onset of these perturbations, a large error is experienced; but with repeated practice these errors gradually decrease. Although multiple learning processes have been shown to be at play during learning, leading to changes in overall behavior through processes such as reaiming (Martin et al., 1996b; McDougle et al., 2015; Redding & Wallace, 1996; Taylor et al., 2014; Weiner et al., 1983), the majority of research has centered on how sensorimotor mappings are altered through adaptation. When the perturbation is removed and participants are asked to move directly to the target, their movements continue to deviate to counter the perturbation. These persistent aftereffects are taken as evidence of "true" sensorimotor adaptation of the mapping (for a review, see McDougle et al., 2016).

An internal forward model, which predicts the sensory consequences of an action, is thought to underlie this adaptation process (Wolpert & Miall, 1996; Wolpert & Kawato, 1998). A common method for investigating sensorimotor adaptation is to introduce a visuomotor rotation, where visual feedback is shifted by rotating it

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relative to the start position. For example, if the target was at 0° (to the right), the participant's hand would reach toward 0°, but the cursor would travel 45° in the counterclockwise direction (up and to the right). However, with repeated exposure to the rotation a participant will learn to reduce this error by moving their hand clockwise of the target, with a reach 45° clockwise of the target (down and to the right) fully countering the perturbation to get the visual feedback on the target. The presence of this visually rotated feedback results in a mismatch between the predicted and actual sensory consequences of a movement, which is thought to lead to a sensory prediction error (Wolpert & Kawato, 1998; Wolpert & Miall, 1996). With training, this prediction error is thought to update the forward model to reduce the discrepancy between the desired motor command and the resultant feedback (Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007).

What is less clear is the precise information conveyed by the sensory prediction error: It may be only binary, signaling simply the presence of an error, or it could carry more rich information regarding features of the error itself. Computational theories have tended toward the latter, assuming that the sensory prediction error conveys both the direction and magnitude of the error (Jordan & Rumelhart, 1992; Ghahramani, Wolpert, & Jordan, 1997; Thoroughman & Shadmehr, 1999). This vectorial information should result in learning that is proportional to the size of the error experienced (Abeele & Bock, 2001). However, experimental results have challenged the motor system's sensitivity to error magnitude information under specific conditions. In visuomotor rotation tasks, trial-by-trial adaptation appears to be insensitive to error size: As the size of the visuomotor rotation increases the size of the adapted response rapidly plateaus (Marko et al., 2012; Wei & Körding, 2009). Additionally, regardless of the size of a rotation, the final, asymptotic level of adaptation does not appear to increase beyond a range of 15° to 25° (Bond & Taylor, 2015; Morehead et al., in press).

Similar characteristics have been found in studies of force field adaptation. Trial-by-trial adaptation to laterally displacing force pulses appears to only be sensitive to the direction of the force pulse, but not its magnitude (Fine & Thoroughman, 2006). In fact, the adapted response appears much more stereotyped than previously thought, appearing nearly identical across a range of force and visuomotor perturbations (Wei & Körding, 2009). Sensitivity to error size only begins to emerge when perturbations are delivered more frequently, or otherwise become more predictable (Fine & Thoroughman, 2006; Semrau, Daitch, & Thoroughman, 2012), which may reflect the operation of other learning processes (Bond & Taylor, 2015; Morehead et al., in press).

It is important to note that not all forms of error-based feedback appear to update the forward model, resulting in adaptation. In visuomotor rotation tasks, reward-based feedback can drive performance improvements during training, but result in negligible aftereffects and reduced sensorimotor remapping compared with error-based feedback in the form of a circular cursor representing the virtual position of the hand in the visual display (Brudner et al., 2016; Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015). Cursor feedback appears to be critical in driving adaptation of the forward model. Indeed, even slight delays between motion of the limb and motion of the cursor can significantly reduce the degree of adaptation, measured via aftereffects (Brudner et al., 2016; Held & Durlach, 1989; Held et al., 1966; Honda et al., 2012; Kitazawa, Kohno, & Uka, 1995; Kitazawa & Yin, 2002). Further, adaptation can occur despite it being irrelevant (Morehead et al., in press; Schaefer et al., 2012) or counter to task goals (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011).

These results raise an important question: What information is uniquely conveyed by cursor feedback which gives rise to sensory prediction errors? Further, which component of the sensory prediction error results in the training of a forward model and resulting aftereffects? Although continuous cursor feedback can result in a stronger degree of adaptation, endpoint cursor feedback alone is sufficient to drive adaptation (Taylor et al., 2013, 2014). From a geometrical perspective, endpoint feedback contains two components of information: the direction and magnitude of the error. Here, in a series of experiments, we sought to identify what form of a visuospatial error was necessary to induce adaptation (i.e., aftereffects) in a visuomotor rotation task. In the first experiment, we show that cursor feedback induced stronger adaptation than scalar feedback (reward- or point-based feedback). In Experiments 2 through 4, we isolated the magnitude and direction components of cursor error to identify which was necessary for adaptation. In Experiment 5, we determined if implicit motor adaptation or explicit aiming were selectively sensitive to the magnitude and direction components of the error signal. Across these five experiments, we find that directional error information is necessary to update a forward model, but not error magnitude. These results challenge current models of sensorimotor adaptation that rely on error magnitude, such as gradient descent algorithms.

Experiment 1: Cursor and Scalar Feedback

Method

Participants. Twenty-four participants (13 female; ages 18 to 22 years) were recruited from the human research participation pool maintained by the Department of Psychology at Princeton University and were compensated with either course credit or payment in exchange for their involvement in the study. This sample size was chosen based on a power analysis using previous results (see following text). All participants had normal or corrected to normal vision and were verified to be right-hand dominant using the Edinburgh Handedness Inventory (Oldfield, 1971). Experimental protocols were approved by the Institutional Review Board at Princeton University and written informed consent was provided by each individual prior to involvement in the study.

Apparatus. Participants made reaching movements to visually displayed targets while seated at a table with their right hand resting comfortably on the surface of the table (Figure 1A). Participants wore a glove on their hand to reduce the friction between their hand and the table, permitting a smooth sliding motion as they reached across the surface of the table. A back-projection screen was positioned horizontally 48 cm above the table and a mirror was mounted halfway between the two. An ultrashort throw monitor projector (Brightlink, Epson, Long Beach, CA) was used to present visual displays onto the projection screen which were then reflected by the mirror. A participant viewed the visual display by looking down on to the mirror, resulting in the illusion that the visual display was in the plane of the table. The mirror also occluded vision of the hand. A sensor was placed on the tip of the index finger and position information was sampled at 100 Hz with

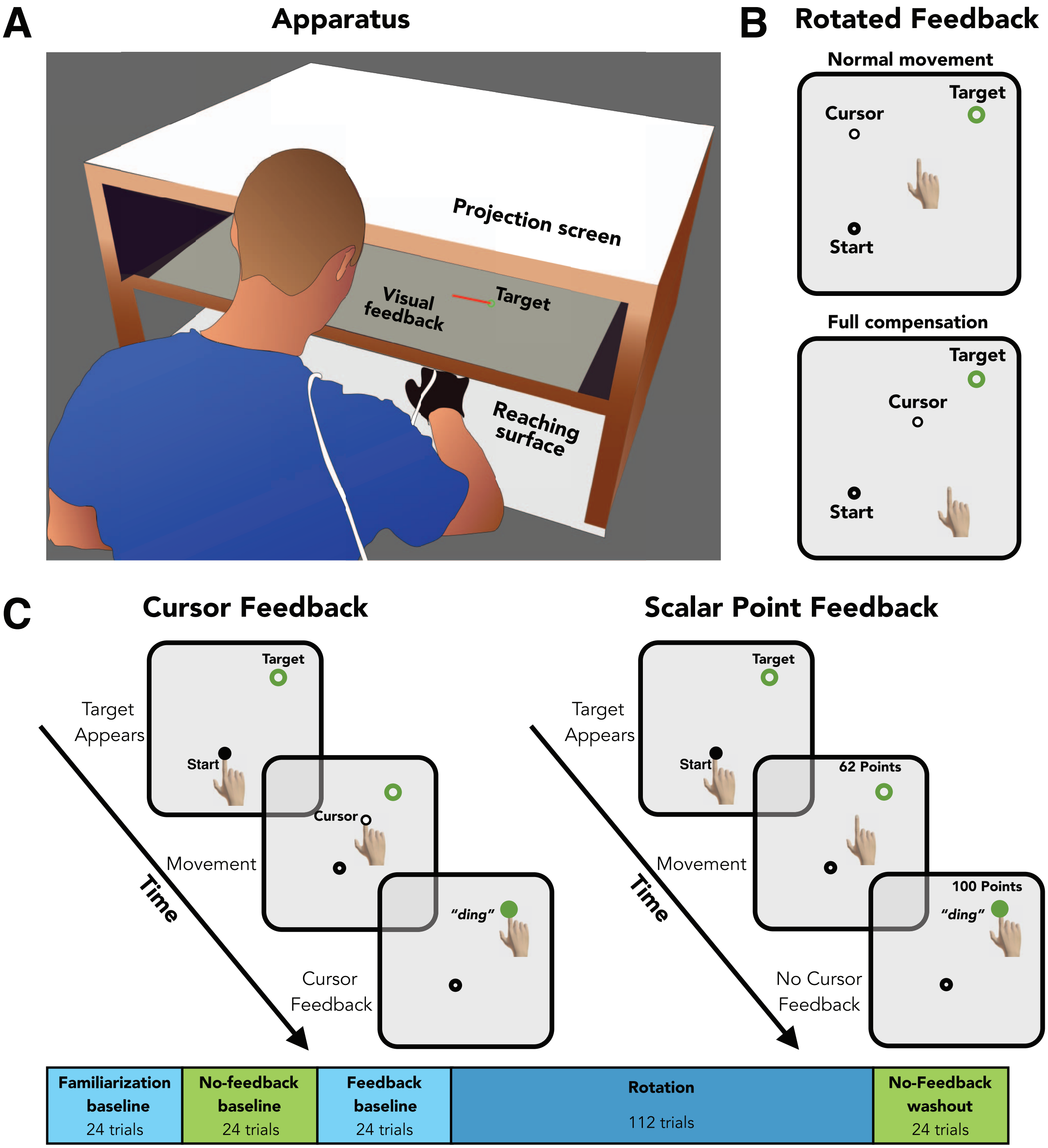

Figure 1. Experiment 1 task design. (A) Participants made reaching movements on a table surface while looking down in to a mirror that blocked the view of their hand. Note, the example feedback shown here pertains to Experiments 2 through 5. (B) Example rotated cursor feedback. (C) Online feedback was provided continuously until the virtual cursor was on the target. In the *scalar* point group, participants did not see their virtual cursor, rather they were continuously presented with points that scaled from 0, *at the start position*, to 100, *when the cursor reached the target*. In the *cursor* group participants were able to see the virtual cursor. Visual feedback of the actual hand position was not available to participants, and is only provided here for clarity in explaining the visual feedback.

an approximate spatial resolution of 0.05 cm using a 3D motion tracking system (trakStar, Ascension Technology, Burlington, VT). Visual displays were controlled using custom software implemented in Python (www.python.com).

Procedure. Each trial began with the participant placing their hand within a start position (1-cm diameter circle). Participants were guided to the start position by a larger circle, centered on the start position, whose radius represented the distance between the cursor and the start position. Thus, as the participant moved their hand closer to the start position, the circle would get continually smaller, guiding the hand to the start position. Initially the start position was represented by an open circle, but became a solid circle to indicate their hand was 1 cm, or less, from the center of the start position. At no point during this guiding procedure was the participant provided with a cursor representing the exact location of their hand, ensuring no information about the visuomotor rotation was gained while finding the start position.

After holding their hand within the start position for 1.5 s, a green target (1.6-cm diameter open circle) was displayed at one of eight locations (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°) at a distance of 10 cm from the start position. The targets were presented in a pseudorandom order such that, within a block of eight trials, the target location was random, while also ensuring the same target was never used twice in a row. As we were specifically interested in the effect on adaptation, participants were required to terminate the cursor in the target region on each trial and were provided with a form of online feedback throughout the movement (described in the following text). Although a form of endpoint feedback would simplify the error signal available to the participants, our goal here was to vary the amount of information in feedback between groups and, given this, it is possible that some participants may not learn how to counter the perturbation. Thus, the requirement to terminate within the target region ensures that any differences in adaptation between groups are not due to differences in simply finding the solution to counter the rotation.

Participants were divided evenly into two experimental groups *cursor* feedback and *scalar* feedback (see Figure 1C). In the *cursor* feedback group, participants were given online cursor feedback in the form of a 1-cm diameter solid white circle. The circular cursor did not appear until they left the start position, after which, online feedback was provided. Once the cursor was placed in the target, the final cursor position remained frozen for 2 s before being removed to start the next trial. In the *scalar* feedback group, participants received online feedback in the form of points: defined by the distance between their cursor and the target location, such that 0 points was displayed when the hand was at the starting location, increasing to 100 points when the unseen cursor was at the target location. By using this constantly updating feedback, participants could guide their hand to the target location by moving their hand toward the direction resulting in increasing points, or away from decreasing points. During an initial familiarization period, the *scalar* feedback group also received online cursor feedback for eight trials, followed by a further eight trials where the cursor was only shown when it was placed on the target at the end of the trial, where it was frozen in place for 2 s. After this familiarization period, all forms of *scalar* feedback were removed and the *scalar* feedback group only received points reflecting the distance to the target.

Each trial ended when the participant placed their cursor within the target, defined as being within 4° of the target angle at a radius of 9.2 cm to 10.8 cm from the start position. At this point the target became solid green and an auditory "ding" was played. Participants were encouraged to make fast reaching movements. If a reach did not terminate within the target location in under 1 s, then the participant received auditory feedback indicating that the movement was "too slow." To keep participants motivated, a summary screen was shown roughly every 40 trials informing them of the percent of trials that had reached the target within the correct time window.

The experiment was divided into five blocks: familiarization baseline, no-feedback baseline, baseline, rotation, and no-feedback washout. When present, participants received visual feedback based on their experimental group (either *cursor* or *scalar*). First participants completed a familiarization baseline block of 24 trials with veridical feedback to get accustomed to the reaching task. Next participants completed 24 trials of a no-feedback baseline block to measure any directional biases in participants' reaching movements (Ghilardi et al., 1995). Unlike other phases of the experiment, participants did not terminate the reach within the target location. Instead, the participants were informed that they would not receive any visual or auditory feedback other than hearing a "knock" sound when they had reached out the distance to the target and, as such, would not know if they hit the target. As no visual feedback was provided, participants were told they did not need to stop on the target location, but should make a shooting movement through the target. This ensured that the participant reached far enough despite the lack of visual feedback. This procedure allowed us to measure reaching behavior without feedback related corrections (see the following text). Finally, in the baseline block, veridical online feedback was restored for an additional 24 trials and participants were required to again terminate their reach within the target location.

Following the three baseline blocks, a 45° counterclockwise rotation (Figure 1B), centered around the start position, was imposed for 112 trials. Thus, to fully counter this rotation and get their virtual cursor on the target, a participant needed to move their hand 45° clockwise of the target location. After the rotation block, participants completed a no-feedback washout block of 24 trials, which was identical in procedure to the no-feedback baseline block. Participants were told to aim directly to the target location and to make shooting movements, as they had practiced in the no-feedback baseline block. Additionally, participants were instructed to stop using any strategies that they may have previously developed. Aftereffects of the perturbation were quantified by comparing the no-feedback baseline and washout blocks. This procedure differed from that used during feedback trials, which required terminating the cursor on the target, to allow for the measurement of aftereffects without the presence of feedback corrections, nor concurrent learning of the unrotated cursor (Taylor et al., 2014). Between all blocks except for between the baseline and rotation blocks, a roughly 20-s break took place while instructions for the next phase were given. The next block began immediately after the participant indicated they understood the instructions. There was no break or noticeable transition between the baseline and rotation blocks.

Data analysis. All initial data analyses were performed with custom scripts written in MATLAB (MathWorks, Natick, MA).

Individual participant means were then submitted to either a one-way or repeated measures analysis of variance (ANOVA) using SPSS (IBM Corp., 2011). Task performance was assessed by calculating the angular difference between the target and the initial heading angle of the hand. The initial heading angle of the hand was calculated by finding the samples taken between 1 cm and 3 cm radially from the start position and calculating the angle between the first and last samples. The presence of online visual feedback, and the requirement that the virtual cursor is placed on the target to end each trial, encourage corrective movements in this task. The use of initial heading angle as the dependent measure allows for a measure of forward model learning before any corrective movements are made. Heading angle was also calculated for all no-feedback trials so that performance in blocks with feedback and without feedback trials was based on the same metric. An exponential function was not fit to the time series of hand angles during the rotation block because participants' learning curves are frequently nonmonotonic (Gallistel et al., 2004; Taylor et al., 2014).

To enable averaging across trials, movement trajectories were rotated to a common axis, as though the intended target was always located at 0°. With this convention, a positive angle is an error in the clockwise direction, whereas a negative angle indicates an error in the counterclockwise direction. Heading angles are reported in hand space, rather than target error, and with this convention the hand angle will increase to compensate for the rotation. To remove any consistent reaching biases during trials with feedback, we subtracted the mean heading angle of the 24 trials in the baseline block from the heading angles on each trial during the rotation block. Likewise, the mean heading angle of the 24 trials in the no-feedback baseline block were subtracted from the heading angles on each trial during the no-feedback washout block. As the order of targets was varied across participants, and biases vary depending on the target direction, for each individual, trials were averaged into bins of eight trials. In this manner, means across individuals are comparing a full cycle of the eight targets. All graphs are plotted using the binned means.

Using these bias corrected values for each individual, the mean hand angle was then calculated for three different epochs of interest: (1) The first eight trials of the rotation block (early rotation), (2) the last eight trials of the rotation block (late rotation), and (3) the first eight trials of the no-feedback washout block. Time to target was also calculated for each trial, defined as the amount of time between the cursor leaving the start position and reaching the target. Trials were excluded from further analysis if the time to target or heading angle for that trial was more than 3 standard deviations from that participant's mean, as these trials were likely to represent grossly erroneous movements. This was done separately for each of the five blocks. This resulted in 2.5% and 3.1% of trials being removed in the cursor and scalar feedback groups, respectively. F values (or t values) and effect size estimates are reported for all comparisons to aid in an analysis that goes beyond just simple p values (Halsey et al., 2015).

Power analysis. For Experiments 1 through 3, the number of participants was chosen on the basis of a convention of 10 to 12 participants in visuomotor adaptation experiments, to be conservative we opted to recruit 12 participants per group. This sample size is consistent with a power analysis performed in a previous of study of ours (Brudner et al., 2016), where delayed cursor feedback was shown to result in impaired adaptation. When compared with a group with no delay in their cursor feedback an effect size of $\alpha = 1.6$ was found. Using this effect size, an independent samples t test using a two-tailed alpha of 0.05 and power of 0.95 suggests that a sample size of 12 participants per group is needed.

Results and Discussion

Participants in both *cursor* and *scalar* groups performed well during the baseline block, however, a small, but consistent, clockwise error in heading angle was present in both groups (*cursor*: 1.4 ± 0.3°; *scalar*: 1.5 ± 0.7°; group comparison: $t_{22} = 0.1$, $p = .94$, $\alpha = 0.05$). Similarly, there was a small clockwise bias in the heading angle during the no-feedback baseline block in both groups (*cursor*: 2.6 ± 0.4°; *scalar*: 1.6 ± 1.0°; group comparison: $t_{22} = 0.8$, $p = .41$, $\alpha = 0.4$). The bias correction procedure described earlier was performed for each participant to remove any systematic biases in reach direction.

Both groups adjusted their heading angles to compensate for the introduction of the visuomotor rotation (see Figure 2). To measure the initial and late stages of the learning process we focused on the first eight and the last eight trials of the rotation block. Participants in both groups displayed a small heading angle change over these trials (*cursor*: 9.6 ± 2.9°; *scalar*: 6.3 ± 3.7°). By the end of the rotation block participants in both groups had further altered their heading angles to counter a large portion of the rotation (*cursor*: 28.0 ± 2.9°; *scalar*: 28.2 ± 6.2°). Notably, neither group altered their initial heading angles sufficiently to completely counter the perturbation, despite the requirement to terminate the cursor with the target region. These values were submitted to a repeated-measures mixed factorial ANOVA with factors of group (*cursor*

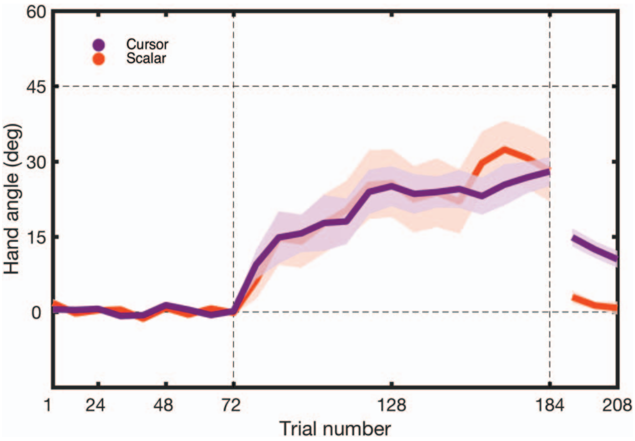

Figure 2. Experiment 1: *Cursor* and *scalar* point feedback performance. Hand heading angle for both *cursor* (purple) and *scalar* (orange) feedback groups. Hand heading angle was calculated by finding the position samples taken between 1 cm and 3 cm radially from the start position, and then calculating the angle between the last and first sample. The vertical dotted lines mark the beginning (Trial 72) and end of the rotation block (Trial 184), although the horizontal dotted lines mark the solution for when no rotation is present (0°) and for countering the rotation (45°). For visualization purposes trials were binned by eight trials (a full cycle of all targets) for each participant, the mean (solid line) and standard error (shaded region) are then plotted for each group.

and *scalar*) and time (early rot and late rot). A main effect of time was present, $F_{(1,22)} = 31.2$, $p < .0001$, $\eta_p^2 = 0.59$, due to both groups increasing their heading angles over the course of the rotation block. No main effect of group, $F_{(1,22)} = 0.1$, $p = .75$, $\eta_p^2 = 0.01$), nor a Group × Time interaction, $F_{(1,\ 22)} = 0.2$, $p = .65$, $\eta_p^2 = 0.01$, were present. Thus, performance was indistinguishable between *scalar* and *cursor* groups.

The heading angle changes are likely a composite of multiple processes involving both stable motor adaptation and more flexible aiming strategies. For an assessment of adaptation, following the rotation block, participants made reaching movements to the target without visual feedback in order to measure the size of any aftereffects from the perturbation. In addition, participants were instructed to aim directly to the target and stop employing any other strategies they may have developed during training. In examining the washout block both *cursor* (14.9 ± 1.8°, $t_{11} = 8.3$, $p < .0001$, $\alpha = 2.4$) and *scalar* (3.0 ± 1.3°, $t_{11} = 2.3$, $p = .04$, $\alpha = 0.7$) participants displayed significant aftereffects, when compared with no aftereffect in a *t* test. However, the size of the aftereffect was significantly larger for the cursor group compared with the scalar group ($t_{22} = 5.4$, $p < .0001$, $\alpha = 2.2$; Figure 2).

In summary, despite comparable performance during the rotation block, participants who received online cursor feedback had significantly more adaptation than participants who received online scalar feedback (i.e., points) to guide them to the target. Even with the addition of online scalar feedback in our task, this result is consistent with previous findings showing a lack of adaptation when feedback was given at the endpoint of a movement, either in the form of scalar points (Nikooyan & Ahmed, 2015), or only binary feedback signaling whether the target was hit (Izawa & Shadmehr, 2011. Why is it that cursor feedback results in sensorimotor adaptation, although scalar feedback does not? One clear difference is that cursor feedback results in a vector error, which provides both the magnitude and direction of the error. Scalar feedback, on the other hand, is an abstract measure of the magnitude of the error, but does not provide any direction information. One possibility is that both components of error are needed to induce motor adaptation (as measured by the size of the aftereffects), and adaptation will not occur when either component is isolated. Another possibility is that direct spatial feedback is necessary for the motor system, and that the motor system does not have access to the scalar feedback due to the abstract nature of the mapping of points to space. Thus, isolated magnitude feedback in the form of a spatial error may be sufficient to induce adaptation.

In Experiment 2, we sought to determine whether isolated magnitude and direction vector components of cursor feedback are able to drive adaptation, or whether both components are necessary. If both components are necessary to drive adaptation then we would expect no adaptation, in the form of an aftereffect, to occur when isolated magnitude or direction spatial feedback are provided. Another possibility is that when the feedback components are isolated, adaptation is partial in both isolated magnitude and direction feedback conditions, which when combined result in the full adaption seen with both components. Alternatively, adaptation may only be sensitive to magnitude or direction information, resulting in full adaptation in one isolated feedback condition, and no adaptation in the other.

Experiment 2: Vector Based Feedback

Method

Participants. An additional 36 participants (28 female; ages 18 to 22 years) were recruited for this experiment and were compensated with either course credit or payment in exchange for their involvement in the study. All participants had normal or corrected to normal vision and were verified to be right-hand dominant. Experimental protocols were approved by the Institutional Review Board at Princeton University and written informed consent was provided by each individual prior to involvement in the study.

Procedure and apparatus. The apparatus and experimental procedures in Experiment 2 were the same as in Experiment 1, except participants were evenly divided into three groups, which differed with respect to the type of online feedback they received while moving to the target (see Figure 3). In the *magnitude plus direction* group, the online feedback consisted of a red line connecting the virtual cursor location to the center of the target, accurately representing the direction and distance of the cursor relative to the target. In the *magnitude only* group, the length of the line accurately reflected the distance between the virtual cursor and the target, but the direction was random and fixed for each trial. For both *magnitude plus direction* and *magnitude only* groups, the participants were told that they would get their "cursor" on the target on each trial by making the red line progressively shorter. In the *direction only* group, the line accurately reflected the direction of the cursor relative to the target, but was a fixed random length for each trial. The *direction only* group was told that since the line was pointing from the target toward the cursor they would hit the target by moving toward the line. For the *direction only* and *magnitude only* groups the length or direction of the line, respectively, was counterbalanced across trials so that all ranges of lengths and directions were equally represented. For the *magnitude only* group the random direction was chosen by dividing the space equally into four quadrants, which were counterbalanced across trials. Once the quadrant was decided for each trial, a random direction was selected within that range using a uniform distribution. In this manner, the direction of the feedback is counterbalanced across trials assuring no consistent direction information is present.

Note that in the *magnitude only* feedback condition the only direct feedback was about magnitude of the error; however, the direction of the error could be indirectly discerned by moving in the direction that shortens the feedback line. In the *direction only* group the random length of the line was chosen by dividing the possible lengths evenly into four ranges. The minimum length of the line was 1 cm, as shorter than this made it difficult to discern the direction the line was pointing. The maximum length of the line was set to 16 cm, as longer than this made the line extend outside the workspace. For each trial in the *direction only* group one of the four length ranges was chosen, and the actual length for that trial was chosen from a uniform distribution in that range. In the *direction only* feedback group the only direct feedback was the direction of the error, however, the magnitude of the error could be indirectly discerned by the amount of movement necessary to cause the line to switch direction. Notably, this would not give any information about the size of rotation, just the proximity of the

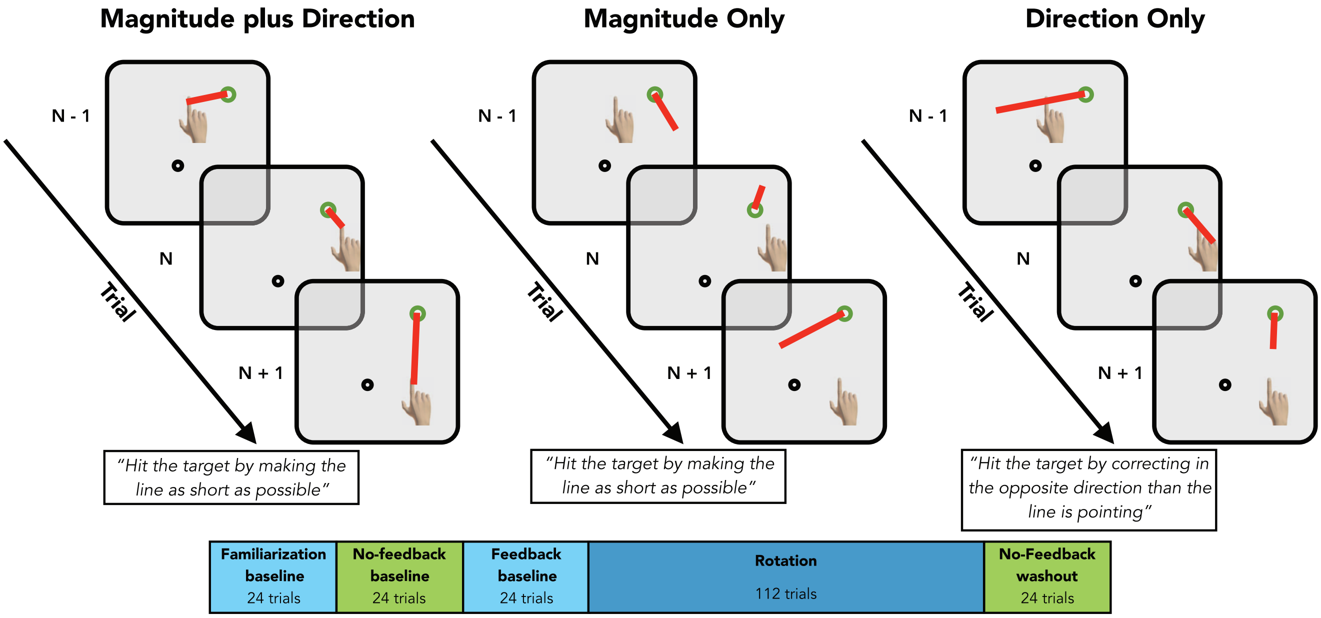

Figure 3. Experiments 2, 3, and 4 task design. The procedure was the same as in Experiment 1, however, three feedback groups were present where participants received visual feedback in the form of a line vector. Three example veridical feedback trials are presented for each group. During the familiarization baseline for all three groups the line accurately represented both the direction and distance of the cursor from the target. The *magnitude plus direction* group continued to receive this feedback for all feedback trials. For the *magnitude only* group, the line correctly represented the distance to the target, but the direction of the line contained no information as it was fixed and random for each trial. In the *direction only* group, the line correctly represented the direction to the target, but the length of the line was fixed and random for each trial. All three groups performed the same no-feedback trials. In Experiment 2, the target appeared at one of eight possible locations, arranged equally around the start position. For Experiment 3, only a single target at 0° (to the right) was used. In Experiment 4 eight target locations were used, but they were arranged in a wedge separated by 2° spanning 82° to 98°, skipping the 90° (straight ahead) location. In Experiments 2 and 3, the trial ended when the cursor was on the target. For Experiment 4, participants were instructed to make shooting movements on all trials, and the trial ended when the cursor exceeded the distance to the target, or if the movement time exceeded 400 ms, whichever happened first.

hand to the solution. When their cursor reached the target all three groups received the same auditory and visual feedback described in Experiment 1. Note that although we refer to the *magnitude only* and *direction only* conditions as only having magnitude and direction error information available, participants could potentially infer the other component via sequential movements. However, since small delays in cursor feedback have been shown to prevent adaptation (Brudner et al., 2016; Kitazawa et al., 1995), we think it is unlikely that the motor system could utilize indirect and largely ambiguous error information that would only be available in a timescale that stretches across trials.

The experiment was divided in to five blocks, as in Experiment 1. During the familiarization baseline block participants in all groups received online *magnitude plus direction* feedback. This ensured that participants were comfortable reaching in the new environment and enabled a consistent no-feedback bias estimate. Following the no-feedback baseline block the group-specific feedback was explained to the participant. After it was confirmed that the participants understood the meaning of the feedback they would receive, a baseline block was performed with this new online visual feedback. The rotation and no-feedback washout block procedures were identical to that in Experiment 1. To remove any consistent reaching biases, the mean heading angle for the 24 trials in the baseline and no-feedback blocks was subtracted from the feedback and no-feedback trials, respectively. Using these bias corrected values for each individual, the mean hand angle was then calculated for three different epochs of interest: (a) The first eight trials of the rotation block (early rotation), (b) the last eight trials of the rotation block (late rotation), and (c) the first eight trials of the no-feedback washout block. Time to target and heading angle data on individual trials resulted in the exclusion of 2.4%, 3.2%, and 3.1% of trials for *magnitude plus direction*, *magnitude only* and *direction only* groups, respectively.

Results and Discussion

In the baseline block all three groups performed well on the task, with only small target errors. The *magnitude plus direction* (2.3 ± 0.7°) and *direction only* (2.1 ± 0.7°) groups both had a small clockwise bias, whereas the *magnitude only* (−0.2 ± 1.3°) group moved closer to the target. A one-way ANOVA performed on these values found no effect of experiment group, $F_{(2,\ 33)} = 2.2$,

$p = .13$, $\eta_p^2 = 0.12$. Likewise, during the no-feedback baseline *magnitude plus direction* (2.1 ± 0.5°) and *direction only* (1.8 ± 0.6°) groups both had a small clockwise bias in heading angle, whereas the *magnitude only* group (0.6 ± 0.6°), on average, moved closer to the target. A one-way ANOVA confirmed no significant differences based on group, $F_{(2,\ 33)} = 2.1$, $p = .14$, $\eta_p^2 = 0.11$. The bias correction procedure was performed on each participant to remove these systematic biases in reach direction.

The introduction of the perturbation caused all three groups to make a small change in their heading angles to compensate for the rotation (*magnitude plus direction*: 7.2 ± 1.8°; *direction only*: 4.9 ± 2.1°; *magnitude only*: 7.5 ± 3.8°; Figure 4A). By the last eight trials of the rotation block participants in all three groups had further altered their initial heading angles to compensate for a large portion of the rotation (*magnitude plus direction*: 21.3 ± 4.7°; *direction only*: 21.3 ± 3.0°; *magnitude only*: 19.0 ± 6.6°). Despite getting to the target on every trial, none of the groups altered their heading angles sufficiently to completely counter the perturbation echoing the results in Experiment 1. These data were submitted to a mixed factorial ANOVA with factors for group (*magnitude plus direction*, *direction only*, and *magnitude only*) and time (early rot and late rot). There was a main effect of time, $F_{(1,\ 33)} = 19.5$, $p = .0001$, $\eta_p^2 = 0.37$, as overall participants increased their heading angles between early and late in the rotation. However, there was neither an effect of group, $F_{(2,\ 33)} = 0.05$, $p = .95$, $\eta_p^2 < 0.01$, nor a Group × Time interaction, $F_{(2,33)} = 0.2$, $p = .82$, $\eta_p^2 = 0.01$. Despite the three groups having different amounts of information in the visual feedback, all three groups learned to alter their hand angles to counter the visuomotor rotation. Further, overall performance was indistinguishable between groups.

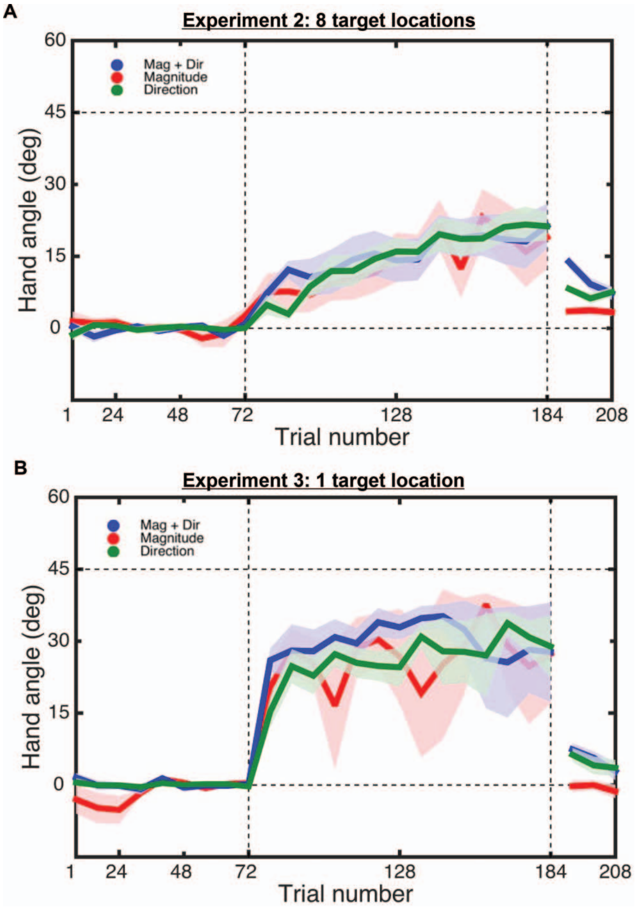

Figure 4. Experiments 2 and 3: Vector based feedback performance. (A) Experiment 2, eight target locations; (B) Experiment 3, 1 target location. Hand heading angle for *magnitude plus direction* (blue), *magnitude only* (red), and *direction only* (green) groups. For visualization purposes, trials were binned by eight trials (a full cycle of all targets) for each participant, the mean (solid line) and standard error (shaded region) are then plotted for each group.

To assess aftereffects from the perturbation participants were instructed to reach directly for the target during the no-feedback washout block. A reliable aftereffect was present in all three groups (*magnitude plus direction*: 13.9 ± 1.3°, $t_{11} = 11.0$, $p < .0001$, $\alpha = 3.1$; *direction only*: 8.2 ± 0.6°, $t_{11} = 14.6$, $p < .0001$, $\alpha = 3.9$; *magnitude only*: 3.5 ± 0.8°, $t_{11} = 4.3$, $p = .001$, $\alpha = 1.3$). To compare the size of the aftereffects between groups, these data were submitted to a one-way ANOVA which revealed a significant difference in adaptation, $F_{(2,\ 33)} = 30.7$, $p < .0001$, $\eta_p^2 = 0.65$, between the three groups. A post hoc comparison confirmed the *magnitude only* group to have a significantly smaller aftereffect than both *magnitude plus direction* ($p < .0001$, $\alpha = 2.8$) and *direction only* ($p = .003$, $\alpha = 1.9$; Bonferroni corrected) groups (Figure 4A). In addition, the aftereffect in the *direction only* group was smaller than in the *magnitude plus direction* group ($p = .0005$, $\alpha = 1.6$; Bonferroni corrected).

These findings indicate that despite all three groups adjusting their heading angles to compensate for the rotation by a comparable amount, visuomotor adaptation significantly differed between the groups. The *magnitude plus direction* group had the most adaptation, with the *direction only* group showing intermediate adaptation and the *magnitude only* group having the least adaptation. The amount of visuomotor adaptation is strikingly similar between the *cursor* (Experiment 1) and *magnitude plus direction* groups, and the *scalar* (Experiment 1) and *magnitude only* groups, whereas the *direction only* group falls in-between. Aftereffects were significantly larger when direction information was provided, either through *direction only*, *magnitude plus direction* or *cursor* feedback, than when isolated magnitude feedback was provided (*scalar* points or *magnitude only*).

Time to target. Performance feedback in the task was based on getting the cursor on the target within the time criterion. Thus, time to target and the rate of task reward (auditory feedback) are inextricably linked in this task. Because each trial did not end until the participant placed their cursor on the target, each trial does not necessarily consist of a single reaching movement, but likely involves an initial movement toward the target and then possibly many corrective movements to get to the target. One concern is that time to target may affect adaptation. A longer time to target will naturally lead to a larger intertrial interval, and a longer total experiment time, resulting in less adaptation (Brennan & Smith, 2015; Hadjiosif et al., 2014). However, the reverse argument could also be made, a longer time to target likely reflects more individual reaching movements toward the target. If so, more samples in the perturbed environment would be expected to lead to more adaptation (Huang & Shadmehr, 2007).

To address this issue, we calculated the median time to target during the rotation block for each participant. The *magnitude plus* *direction* group had the shortest mean time to target of 0.9 ± 0.06s, whereas for the *direction only* group it was longer at 2.5 ± 0.21s, and for the *magnitude only* group it was the longest at 4.7 ± 0.39s. A one-way ANOVA on these values with a factor for group (*magnitude plus direction*, *direction only*, and *magnitude only*) confirmed a significant effect of group, $F_{(2,\ 33)} = 54.4$, $p < .0001$, $\eta_p^2 = 0.77$. A post hoc comparison confirmed the *magnitude only* group to have taken a significantly longer mean time to target than both *direction only* ($p < .0001$, $\alpha = 2.0$) and *magnitude plus direction* ($p < .0001$, $\alpha = 3.9$) groups, whereas *direction only* also took significantly longer than the *magnitude plus direction* ($p = .0004$, $\alpha = 3.1$) group.

As there is both a difference in time to target and adaptation between the three groups, the reduced aftereffect could simply be a function of time, a possibility we explore in Experiment 3. Although aftereffects were present in all groups, they were very small. To increase the degree of adaptation, as measured by the size of the aftereffect, we sought to have participants train at only a single target location in Experiment 3 because training to a single target has previously been shown to result in stronger adaptation (Bond & Taylor, 2015). It has been theorized that learning in adaptation paradigms may have a temporally stable and unstable component, with the latter decaying until a target location is repeated (Hadjiosif et al., 2014). Thus, training at a single location is thought to result in stronger adaptation due to decreased time between repeated movements to an individual target location. If the lack of adaptation seen in the *magnitude only* group was due to a longer time-to-target, compared with the other two groups, we would expect a reduced time to target when using only a single target location and, as a consequence, increased adaptation for this group. However, if sensorimotor adaptation does not rely on magnitude information, we would expect minimal adaptation in the *magnitude only* group.

Experiment 3: Single Target Vector Based Feedback

Method

Participants. An additional 36 participants (16 female; ages 18 to 22 years) were recruited for this experiment and were compensated with either course credit or payment in exchange for their involvement in the study. All participants had normal or corrected-to-normal vision and were verified to be right-hand dominant. Experimental protocols were approved by the Institutional Review Board at Princeton University, and written informed consent was provided by each individual prior to involvement in the study.

Procedure and apparatus. The procedures and apparatus for Experiment 3 are identical to those in Experiment 2, except only a single target location (at 0°) was used. Using bias corrected values for each individual, the mean hand angle was again calculated for three different epochs of interest: (1) The first eight trials of the rotation block (early rotation), (2) the last eight trials of the rotation block (late rotation), and (3) the first eight trials of the no-feedback washout block. Time to target and heading angle data on individual trials resulted in the exclusion of 3.0%, 3.6%, and 3.6% of trials for *magnitude plus direction*, *magnitude only*, and *direction only* groups, respectively.

Results and Discussion

In the baseline all three groups had only small target errors. The *magnitude plus direction* (1.2 ± 0.8°) and *direction only* (2.3 ± 1.0°) groups both had a small clockwise bias, while the *magnitude only* (6.7 ± 2.8°) group had a slightly larger clockwise bias. A trend was present with a one-way ANOVA for a difference based on group, $F_{(2,\ 33)} = 2.8$, $p = .08$, $\eta_p^2 = 0.14$, however, note that our measure of adaptation is compared with the no-feedback baseline. During the no-feedback baseline all three groups had a small clockwise bias, with no differences between the groups (*magnitude plus direction*: 1.3 ± 1.6°; *direction only*: 2.7 ± 1.9°; *magnitude only*: 4.0 ± 1.7°; one-way ANOVA: $F_{[2,\ 33]} = 0.6$, $p = .56$, $\eta_p^2 = 0.04$). To correct for any systematic biases, the bias correction procedure was performed for each participant.

All three groups adjusted their hand heading angles to compensate for the introduction of the rotation (*magnitude plus direction*: 26.0 ± 2.5°; *direction only*: 15.3 ± 3.3°; *magnitude only*: 20.5 ± 5.0°). Note that, compared with Experiment 2, the use of only a single target resulted in participants compensating for a large portion of the rotation during these early rotation trials (Figure 4B). Despite this faster early learning, by the end of the rotation block participants in all three groups had still only countered roughly half of the rotation (*magnitude plus direction*: 27.7 ± 10.4°; *direction only*: 28.8 ± 6.5°; *magnitude only*: 27.4 ± 10.3°). An ANOVA of these values revealed no effect of group, $F_{(2,\ 33)} = 0.2$, $p = .83$, $\eta_p^2 = 0.01$, time, $F_{(1,\ 33)} = 2.1$, $p = .16$, $\eta_p^2 = 0.06$, nor a Group × Time interaction, $F_{(2,\ 33)} = 0.5$, $p = .64$, $\eta_p^2 = 0.03$.

Following the rotation block, participants completed a no-feedback washout block where they aimed directly at the target to measure aftereffects. A reliable aftereffect was present in *magnitude plus direction* (7.4 ± 1.3°, $t_{11} = 5.7$, $p < .0001$, $\alpha = 1.6$) and *direction only* groups (6.3 ± 1.5°, $t_{11} = 4.3$, $p = .001$, $\alpha = 1.2$), but not in the *magnitude only* group (−0.2 ± 1.3°, $t_{11} = 0.2$, $p = .86$, $\alpha = 0.04$). A group comparison of the aftereffect data with a one-way ANOVA resulted in a significant group effect, $F_{(2,\ 33)} = 9.4$, $p = .001$, $\eta_p^2 = 0.36$. A post hoc comparison confirmed the *magnitude only* group, to have a significantly smaller aftereffect than both *magnitude plus direction* ($p = .001$, $\alpha = 1.7$) and *direction only* groups ($p = .005$, $\alpha = 1.3$**;** Bonferroni corrected; Figure 4B). Unlike Experiment 2, however, there was no difference between *magnitude plus direction* and *direction only* groups ($p = 1.0$, $\alpha = 0.2$; Bonferroni corrected).

As in Experiment 2, despite all three groups adjusting their heading angles a comparable amount to compensate for the rotation, the *magnitude only* group had significantly less adaptation. In fact, with the use of only a single target the *magnitude only* group had no measurable adaptation. This again suggests an impairment in visuomotor adaptation when isolated magnitude feedback is given, while adaptation is preserved with isolated direction feedback. Further, *magnitude plus direction* feedback does not appear to show any benefit to visuomotor adaptation over isolated direction feedback.

Time to target. In Experiment 2 there was a significant relationship between time to target and the amount of adaptation. For Experiment 3, a one-way ANOVA on median time to target found no difference in time to target, $F_{(2,\ 33)} = 2.0$, $p = .15$, $\eta_p^2 = 0.11$, between *magnitude plus direction* (0.7 ± 0.08s), *direction only* (1.4 ± 0.35s), and *magnitude only* groups (0.9 ±

0.25s). Notably, the *direction only* group had the longest time to target, but had comparable aftereffects to the *magnitude plus direction* group. The use of only a single target reduced the time to target, compared with Experiment 2, for all participants. Thus, time to target does not appear to explain the lack of adaptation in the *magnitude only* feedback group as it did not differ between the three groups.

The results of Experiments 2 and 3 suggest that information regarding error magnitude results in either weak or no adaptation. To increase adaptation, and to simplify the solution, we provided on each trial online feedback until the cursor was on the target, at which point the trial was complete. By using this procedure, participants are quite likely making feedback corrections to get their cursor on the target. One concern is that the group differences we observed were not due to differences in visual feedback per se, but rather arose from differences in feedback corrections, as previous work has suggested that the feedback correction may drive adaptation (Kawato, 1996; Albert & Shadmehr, 2016). In Experiment 4, we sought to address this concern by modifying the task design so that participants made a single ballistic movement toward the target on each trial, reducing the potential for feedback corrections. If the lack of adaptation observed in the *magnitude only* group, compared with the other groups, was the result of different feedback corrections between groups, then adaptation may be restored. However, if direction information is necessary for adaptation, we would predict similar and substantial adaptation in the *direction only* and *magnitude plus direction* groups, but a lack of adaptation in the *magnitude only* group.

Experiment 4: Shooting Movements With Vector Based Feedback

Method

Participants. An additional 61 participants (37 female; ages 18 to 35 years) were recruited for this experiment (see the following Power Analysis section) and were compensated with either course credit or payment in exchange for their involvement in the study. Seven participants were excluded for having too many slow movements (see the following text), resulting in a final dataset of 54 participants who were evenly distributed between the three groups. All participants had normal or corrected to normal vision and were verified to be right-hand dominant. Experimental protocols were approved by the Institutional Review Board at Princeton University and written informed consent was provided by each individual prior to involvement in the study.

Procedure and apparatus. The procedures and apparatus for Experiment 4 are identical to those in Experiment 2, except as noted here. Eight target locations were again used, however, they were spread from 82° to 98° with 2° spacing, skipping 90° (straight ahead). This target arrangement both simplifies the solution, compared with eight targets arranged in a circle, while also ensuring that the same movement is not repeated on every trial, as is the case with a single target. As our focus was on the aftereffects resulting from the differences in visual feedback, not the learning of the perturbation, more specific instructions were given. Participants were instructed that at some point the mapping between their hand and the cursor would change, resulting in needing to use the visual feedback to figure out which side of the target and how far to that side to move their hand to get their cursor on the target. To control for any directional biases (Ghilardi et al., 1995) when using targets that cover only a small portion of the workspace, half of the participants received a 45° counterclockwise rotation (as in Experiments 1 through 3), whereas the other half of the participants received a 45° clockwise rotation.

Our primary concern was to ensure that any aftereffects present were a result of the rotated visual feedback, and not due to the presence of movement corrections made to counter the online feedback. Three adjustments were made to the task design. First, to minimize feedback corrections, participants were instructed to make quick shooting movements toward the target on each trial. Second, whereas in Experiments 1 through 3 participants had to place their cursor on the target to end the trial, in Experiment 4 the trial ended when the radial distance of the cursor from the start position exceeded the distance to the target, at which point all visual feedback was removed. If the cursor intersected the target, defined as being within 4° of the target angle, the same auditory “ding” was played as in Experiments 1 through 3. However, if the cursor did not intersect the target a mildly aversive “buzz” was played. Finally, to further reduce feedback corrections, if the cursor did not travel a radial distance of 10 cm from the start position—the distance to the target—within 400 ms, all visual feedback was removed and the words “Too Slow!” appeared on the screen along with auditory feedback “too slow.” Thus, if a participant tried to stop and make a feedback correction, the visual feedback would disappear before they were able to complete the correction. Seven participants (6 female) were excluded from further data analysis for having movements that were too slow on more than 10% of trials during the rotation phase (*magnitude plus direction*: 3; *magnitude only*: 3; *direction only*: 1). In the remaining participants, the presence of feedback corrections in each trial was measured by looking at the difference between the hand heading and end angles. After bias correction for each individual, the mean hand angle was then calculated for three different epochs of interest: (a) the first eight trials of the rotation block (early rotation), (b) the last eight trials of the rotation block (late rotation), and (c) the first eight trials of the no-feedback washout block. Last, time to target and heading angle data on individual trials resulted in the exclusion of 8.1%, 7.3%, and 5.9% of trials for *magnitude plus direction*, *magnitude only*, and *direction only* groups, respectively.

Power analysis. For Experiments 4 and 5, we used the results from Experiments 2 and 3 to estimate the minimum sample size required to detect an expected effect size. Specifically, we focused on one “pure” measure of adaptation, the magnitude of the aftereffect during the no-feedback washout block, comparing these measures for the *magnitude only* and *direction only* groups. Power was estimated for an independent samples t test, using a two-tailed α of 0.05 and power of 0.95. On the basis of our initial analyses, the group means and standard deviations for the no-feedback washout trials in Experiment 2 and 3 resulted in an effect size of $\alpha = 1.9$ ($\alpha_{\text{Mag only}} = 3.5°$, $\sigma_{\text{Mag only}} = 2.8°$, $\alpha_{\text{Dir only}} = 8.2$, $\sigma_{\text{Dir only}} = 2.1°$) and $\alpha = 1.27$ ($\alpha_{\text{Mag only}} = 0.4°$, $\sigma_{\text{Mag only}} = 3.7°$, $\alpha_{\text{Dir only}} = 6.7$, $\sigma_{\text{Dir only}} = 6.0°$), respectively. To be conservative, we opted for the smaller effect size from Experiment 3, resulting in a sample size of 18 participants per group.

Results and Discussion

All three groups performed well on the task during the baseline block, with only small target errors. The *magnitude plus direction* (1.4 ± 0.3°) and *direction only* (2.1 ± 0.7°) groups both had a small clockwise bias, while the *magnitude only* (−0.5 ± 1.8°) group moved closer to the target. A one-way ANOVA confirmed no differences were present based on group, $F_{(2,\ 51)} = 1.4$, $p = .26$, $\eta_p^2 = 0.05$. During the no-feedback baseline *magnitude plus direction* (1.5 ± 0.8°) and *direction only* (2.9 ± 1.2°) groups both had a small clockwise bias in heading angle, while the *magnitude only* group (0.2 ± 1.1°), on average, moved closer to the target (one-way ANOVA: $F_{[2,\ 51]} = 1.5$, $p = .22$, $\eta_p^2 = 0.06$). The bias correction procedure was performed on each participant to remove any systematic biases in reach direction. The direction of the visuomotor rotation was counterbalanced across participants, so that for some participants the clockwise bias was in the direction to help counter the rotation, whereas for the other half of participants it was in the opposite direction.

As in previous experiments, after the introduction of the perturbation all three groups made changes in their heading angles to compensate for the rotation (*magnitude plus direction*: 25.6 ± 3.7°; *direction only*: 17.5 ± 2.8°; *magnitude only*: 21.0 ± 4.4°), and by the end of the rotation block all three groups had changed their headings angles to compensate for most of the rotation (*magnitude plus direction*: 47.6 ± 2.0°; *direction only*: 41.7 ± 1.6°; *magnitude only*: 36.6 ± 2.9°; Figure 5A). A mixed factorial ANOVA revealed main effects of group, $F_{(2,\ 51)} = 4.3$, $p = .02$, $\eta_p^2 = 0.14$, and time, $F_{(1,\ 51)} = 67.9$, $p < .0001$, $\eta_p^2 = 0.57$, but no interaction, $F_{(2,\ 51)} = 1.1$, $p = .4$, $\eta_p^2 = 0.04$. Post hoc comparisons revealed the main effect of group to be driven by a difference between the *magnitude plus direction* and both *magnitude only* ($p = .04$) and *direction only* ($p = .05$) groups, whereas no difference was present between *magnitude only* and *direction only* groups ($p = 1.0$; Bonferroni corrected). Although this may seem to suggest an advantage in countering the perturbation when both components of feedback are present, there was no difference between the three feedback groups in Experiments 2 and 3. At best, this advantage is only present when shooting movements are made, and appears to have likely been due to an overcompensation for the rotation in the *magnitude plus direction* group. No differences in hand heading angles over the rotation block were present between the *magnitude only* and *direction only* feedback groups. Regardless, as performance during the rotation block is likely composed of both explicit aiming and implicit learning processes, we consider aftereffects to reflect a purer assessment of adaptation between the groups.

Immediately following the rotation block participants were instructed to reach directly toward the target and completed a no-feedback washout block (Figure 5A). An aftereffect from the visuomotor rotation was present for all three groups (*magnitude plus direction*: 13.2 ± 2.1°, $t_{17} = 6.3$, $p < .0001$, $\alpha = 1.5$; *direction only*: 8.4 ± 1.2°, $t_{17} = 7.2$, $p < .0001$, $\alpha = 1.6$; *magnitude only*: 2.7 ± 1.0°, $t_{17} = 2.7$, $p = .01$, $\alpha = 0.6$). A one-way ANOVA revealed a significant effect of group, $F_{(2,\ 51)} = 12.3$, $p < .0001$, $\eta_p^2 = 0.33$, which a post hoc comparison confirmed was due to a smaller aftereffect in *magnitude only* participants compared with both *magnitude plus direction* participants ($p < .0001$, $\alpha = 1.5$) and *direction only* participants ($p = .03$, $\alpha =$

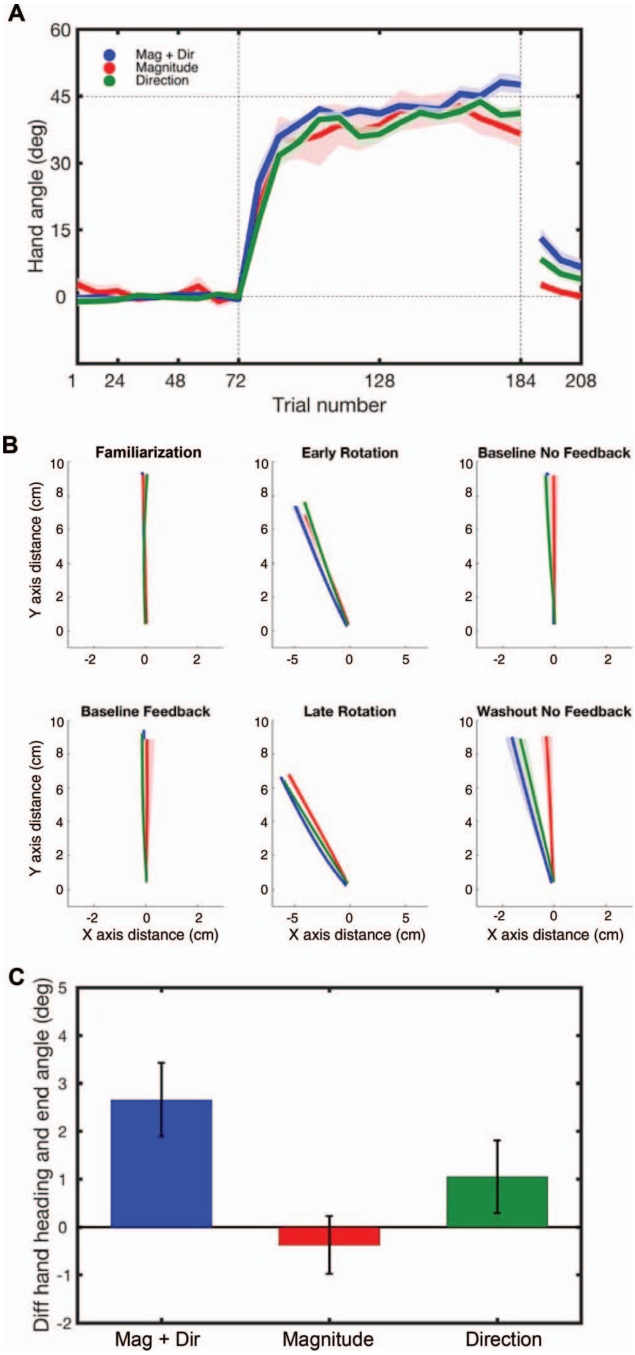

Figure 5. Experiment 4: Shooting movements with vector based feedback. (A) Hand heading angle for *magnitude plus direction* (blue), *magnitude only* (red), and *direction only* (green) groups. For visualization purposes trials were binned by eight trials (a full cycle of all targets) for each participant, the mean (solid line), and standard error (shaded region) are then plotted for each group. (B) Mean trajectories (solid line) and standard error of the mean (shading). Movements are oriented so that, when no rotation is present, the target is straight ahead along the *y*-axis. Mean trajectories were created by taking each individual trial and resampling to 10 total samples by using the cubic spline interpolant. For each block, the mean was calculated for each participant and then the group mean was calculated for the participants in each of the three groups. (C) The mean of the median difference between the hand heading and end angle for each participant over the rotation block. Error bars represent standard error of the mean.

1.2). A trend was also present for *direction only* participants to have a smaller aftereffect than *magnitude plus direction* ($p = .08$, $\alpha = 0.7$) participants.

Despite the change to shooting movements to discourage feedback corrections, participants in all three groups adjusted their heading angles to compensate for the visuomotor rotation, but a significantly larger aftereffect was present in groups that received direction feedback (*direction only* and *magnitude plus direction*). Although a significant aftereffect was present in the *magnitude only* feedback group, this aftereffect is only 3°, which is less than half the size of the aftereffect in the other two groups. This replicates the effect of minimal adaptation when isolated magnitude feedback is provided, however, we wanted to confirm no differences in feedback corrections were present between the groups.

Feedback corrections. Participants, on average, made straight-line movements in all phases of the experiment (Figure 5B), suggesting changes to the experimental procedures to discourage feedback corrections were effective. To quantify the presence of feedback corrections in the rotation block, the difference between the hand heading and end angle was calculated for each trial during the rotation phase and the median for each participant was then compared between groups. Participants in the *magnitude plus direction* (2.7 ± 0.8°), *direction only* (1.1 ± 0.8°), and *magnitude only* (−0.4 ± 0.6°) feedback groups had small differences between heading and end angles, suggesting feedback corrections were minimal (Figure 5C). Despite minimal feedback corrections, a main effect of group, $F_{(2,\ 51)} = 4.5$, $p = .02$, $\eta_p^2 = 0.15$, is found when submitted to a one-way ANOVA. Post hoc comparisons revealed the group effect to be driven by larger corrections in the *magnitude plus direction* participants when compared with *magnitude only* participants ($p = .01$, $\alpha = 1.0$). No differences were present between *direction only* participants and either *magnitude plus direction* ($p = .4$, $\alpha = 0.5$) or *magnitude only* ($p = .5$, $\alpha = 0.5$) participants. Thus, even though the size of feedback corrections were rather small (less than 3°), the *magnitude plus direction* group did have larger corrections than participants in the *magnitude only* group. Importantly, however, there was no difference between the *magnitude only* and *direction only* groups.

In summary, in Experiment 4 we found that differences in the size of the aftereffects between groups is not attributable to feedback corrections. The results of Experiments 1 through 4 strongly suggest that information regarding error magnitude results in either weak or no adaptation. Interestingly, however, in all experiments we found that participants still learn to counter the rotation during the rotation block to nearly an equal degree. How, then, are participants learning to counter the rotation? Recent work from our lab has found that both implicit motor adaptation and explicit aiming are used in combination to counter a rotation (Taylor et al., 2014; Bond & Taylor, 2015). In Experiments 2 through 4, the *magnitude only* feedback groups learned to counter the visuomotor rotation, but showed limited or no adaptation (in the form of aftereffects). This would suggest that participants in the *magnitude only* feedback group are primarily using an explicit aiming strategy to counter the perturbation.

To directly test this idea, in Experiment 5, we asked participants to verbally report their aiming location on each trial so that we can dissociate the operation of implicit motor adaptation and explicit aiming as a function of the information in error feedback. In Experiments 2 through 4 participants in all three groups displayed a precipitous drop, of varying sizes, in hand heading angle between the last eight trials of the rotation block and the first eight trials of the no-feedback washout block. As the no-feedback washout block is a purer measure of adaptation, this drops suggests that, for all participants, performance during the rotation block is likely a combination of explicit aiming and implicit motor adaptation. Given the lack of adaptation we have shown in the *magnitude only* group, we would expect hand heading angle changes during the rotation block to be mainly driven by changes in explicit aiming. Additionally, when we estimate implicit motor adaptation during the rotation block, we would expect to see implicit motor adaptation in the *direction only* and *magnitude plus direction* groups, but again minimal adaptation for the *magnitude only* group.

Experiment 5: Single Target Vector Based Feedback With Verbal Aim Reports

Method

Participants. An additional 54 participants (28 female; ages 18 to 23 years) were recruited for this experiment and were compensated with either course credit or payment in exchange for their involvement in the study. All participants had normal or corrected to normal vision and were verified to be right-hand dominant. Experimental protocols were approved by the Institutional Review Board at Princeton University and written informed consent was provided by each individual prior to involvement in the study.

Apparatus. The experimental procedure and apparatus were altered in Experiment 5 to enable collection of explicit aiming strategies during rotation training. Participants held a digitizing pen in their right hand and made horizontal reaching movements by sliding it on the surface of a digitizing tablet (Intuos Pro Large, Wacom). Position information was sampled at 60 Hz with an approximate spatial resolution of 0.05 cm. Visual feedback was displayed on a 17-in., 1,024 × 768 resolution Dell LCD monitor that was mounted horizontally approximately 25 cm above the tablet. By mounting the monitor in this way, vision of the limb below is occluded.

Procedure. The experimental procedures were similar to those described in Experiment 3, except for the following modifications. Because of the smaller workspace of the setup the distance from the start position to the target was reduced to 7 cm, and the maximum length of the line in the *direction only* group was set to 7.5 cm. In addition, the start position was changed to a 0.4-cm diameter circle and the target to a 0.8-cm circle. The main change in procedure for Experiment 5 is that participants were asked to report their intended aiming direction as described in detail in a previous report (Taylor et al., 2014). For feedback trials, the visual workspace included a ring of numbered "landmarks," spaced at regular 5.6° intervals (see Figure 6). On aiming report trials, prior to each movement, participants verbally reported the landmark they planned to reach toward. These verbal reports were recorded by the experimenter. Trials in which the participant failed to report their aim were excluded from further analysis. Participants in the *magnitude plus direction*, *magnitude only*, and *direction only* groups failed to report their aim on 0.3%, 0.6%, and 0.4% of trials, respectively. To ensure that all participants discovered the

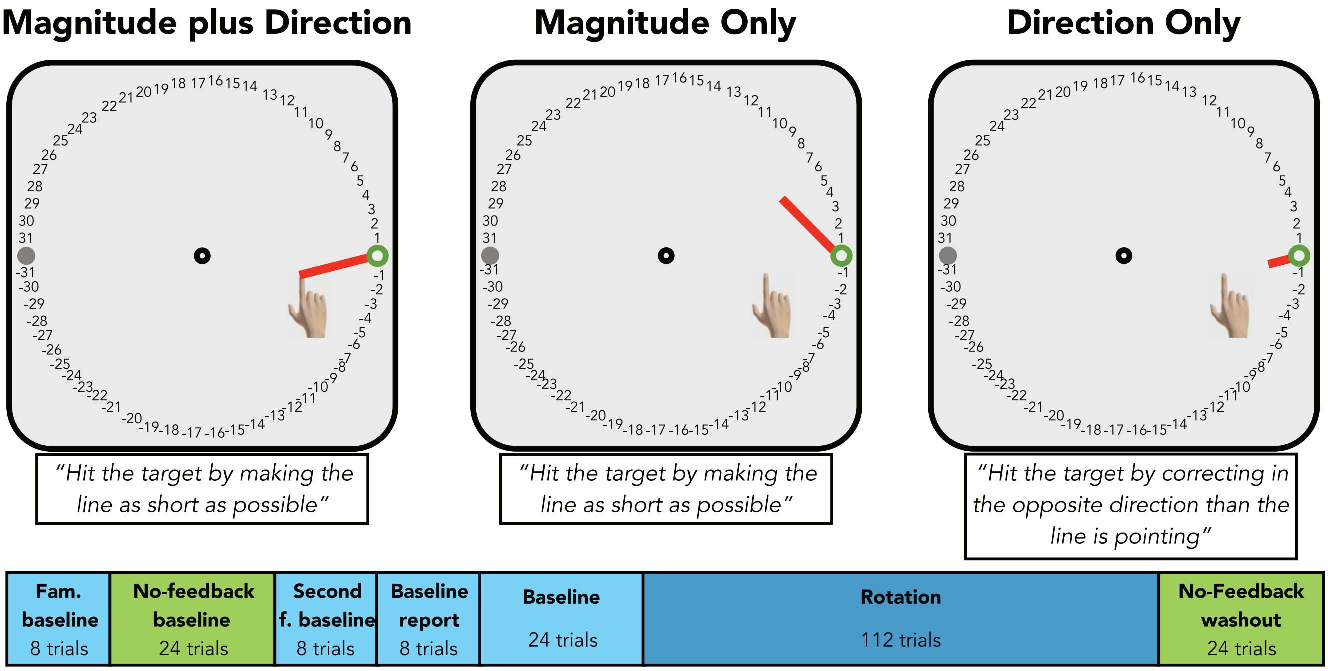

Figure 6. Experiment 5: aiming report task design. The three feedback groups were the same as in Experiments 2 through 4. As in Experiment 3, a single 0° target location was used; however, in addition to the procedures in Experiment 3, participants were asked to report their intended aiming location. On each trial, after the target appeared, but before moving, participants were asked to verbally report which numbered location they were aiming toward to get their cursor on the target.

correct solution, we required participants to get their cursor on the target to terminate each trial, which is the same procedure used in Experiments 1 through 3. Additionally, as in Experiment 3, only a single target location was used.

The experiment was divided into seven blocks: familiarization baseline, no-feedback baseline, a second familiarization baseline, baseline report, baseline, rotation and no-feedback washout. First, participants completed eight trials with veridical feedback where all groups received the online *magnitude plus direction* feedback. After this initial familiarization block, participants completed the 24 trial, no-feedback baseline block. This was then followed by a second familiarization baseline where all groups again received the online *magnitude plus direction* feedback for an additional eight trials. The verbal aim report procedure was then explained to the participant followed by eight trials of the baseline report block. Last, the group-specific visual feedback was described to the participant and the participant was told to continue verbally reporting their aim on each trial. Participants continued to report their aim throughout the baseline and rotation blocks. During both the no-feedback baseline block and the final no-feedback washout block, no visual landmarks were present and participants were told to aim directly at the target.

As in Experiment 4, to control for any directional biases, half of the participants received a 45° counterclockwise rotation, whereas the other half of the participants received a 45° clockwise rotation. The visual landmarks flipped for each participant depending on the direction of the rotation so that reporting a positive number was always in the direction to counter the rotation. After bias calculation, the data from participants who received a clockwise rotation was sign flipped so that it aligned with those receiving a counterclockwise rotation. Using this convention all angles are reported such that a positive angle is in the direction to counter the rotation for that individual participant, and a negative angle is in the opposing direction.

Data analysis. To obtain an estimate of implicit learning, the reported aiming angle was subtracted from the measured hand angle on all verbal report trials. To remove any consistent reaching bias during feedback trials, the baseline bias was calculated for each participant by taking the mean implicit learning estimate of the 24 veridical feedback trials prior to the implementation of the rotation (baseline). The implicit learning estimate was used because the hand angle also reflects any aiming that the participant may use. This bias was then subtracted from both the hand angle and implicit learning estimate for all feedback trials. To remove any reaching bias on trials without feedback, the mean heading angle of the 24 no-feedback baseline trials was subtracted from all no-feedback trials (baseline and washout).

Using these bias-corrected values, the mean hand angle was then calculated on an individual basis for three different epochs: (1) the first eight trials of the rotation block (early rotation), (2) the last eight trials for the rotation block (late rotation), and (3) the first eight trials of the no-feedback washout block. The mean aiming angle and implicit learning estimate were calculated for two different epochs: (1) the first eight trials of the rotation block (early rotation), and (2) the last eight trials for the rotation block (late rotation). Time to target was also calculated for each trial. Trials were excluded from further analysis if the time to target for that trial was more than three standard deviations from that participant's mean, as these trials were likely to represent erroneous movements. Additionally, trials were excluded if the implicit learning estimate for that trial was more than three standard deviations from that participant's mean implicit learning estimate. This was done separately for baseline and rotation trials as movement time and implicit learning are expected to increase when the rotation was present. This procedure resulted in the exclusion of 2.5%, 2.9%, and 2.9% of trials for *magnitude plus direction*, *magnitude only*, and *direction only* groups, respectively.

Results and Discussion

The experimental paradigm was identical to that in Experiment 3, except participants reported which numbered landmark they intended to aim toward before moving on each trial (see Figure 6). Participants were assigned to either the *magnitude plus direction*, *direction only*, or *magnitude only* feedback groups. All three groups moved directly toward the target during the baseline report block with only small heading angle errors (*magnitude plus direction*: 0.2 ± 0.4°; *direction only*: −0.2 ± 0.2°; *magnitude only*: −1.4 ± 0.6°). During the baseline report block participants were also asked to report where they were aiming before moving on each trial. The majority of participants in all three groups reported aiming directly at the target (*magnitude plus direction*: 85%; *direction only*: 85%; *magnitude only*: 65%). Although the *magnitude only* group reported aiming directly at the target less often than the other two groups, 93% of aim reports were either to the target or to a target-adjacent landmark.

A feedback bias was estimated for each participant by subtracting the aim report from the heading angle for each trial in the baseline block, and then taking the mean over the entire baseline block. All three groups had a clockwise bias. A slightly larger bias was present in *magnitude only* (7.2 ± 0.8°) than in *magnitude plus direction* (2.1 ± 0.5°) and *direction only* (3.8 ± 0.6°) participants. A one-way ANOVA revealed a significant effect of group, $F_{(2,\ 51)} = 15.8$, $p < .0001$, $\eta_p^2 = 0.38$, post hoc comparisons found this difference to be driven by a larger bias for the *magnitude only* group compared with *magnitude plus direction* ($p = .00$, $\alpha = 1.8$) and *direction only* groups ($p = .002$; bonferroni corrected, $\alpha = 1.1$). During the no-feedback baseline *magnitude plus direction* (8.2 ± 1.1°), *magnitude only* (6.8 ± 0.8°), and *direction only* (5.7 ± 0.9°) participants all had a clockwise bias (one-way ANOVA: $F_{(2,\ 51)} = 1.7$, $p = .19$, $\eta_p^2 = 0.06$). To remove these systematic biases, the feedback and no-feedback bias estimates were subtracted from all trials with feedback and without feedback, respectively. In addition, the direction of the visuomotor rotation was counterbalanced across participants, so that for some participants the clockwise bias was in the direction to help counter the rotation, whereas for the other half of participants it was in the opposite direction.

The introduction of the rotation induced heading angle changes in all three groups (*magnitude plus direction*: 29.6 ± 2.3°; *direction only*: 16.9 ± 2.9°; *magnitude only*: 15.8 ± 3.6°), with participants further altering their heading angles by the end of the rotation block (*magnitude plus direction*: 43.0 ± 0.5°; *direction only*: 41.9 ± 2.3°; *magnitude only*: 33.3 ± 4.4°; Figure 7A). A main effect of group, $F_{(2,\ 51)} = 6.4$, $p = .003$, $\eta_p^2 = 0.20$, and time, $F_{(1,\ 51)} = 82.7$, $p < .0001$, $\eta_p^2 = 0.62$, was found by an ANOVA, but only a marginal interaction, $F_{(2,\ 51)} = 2.8$, $p = .07$, $\eta_p^2 = 0.10$. Post hoc comparisons revealed the main effect of group to be driven by a difference in performance between the *magnitude plus direction* and *magnitude only* groups ($p = .002$, $\alpha = 0.9$; bonferroni corrected).

Following the rotation, an aftereffect from the visuomotor rotation was present in the no-feedback washout block for both *magnitude plus direction* (10.2 ± 1.3°, $t_{17} = 8.1$, $p < .0001$, $\alpha = 1.9$) and *direction only* (8.5 ± 2.0°, $t_{17} = 4.3$, $p = .0005$, $\alpha = 1.0$) participants, but no reliable aftereffect was present in *magnitude only* participants (1.5 ± 1.6°, $t_{17} = 1.0$, $p = .35$, $\alpha = 0.2$). A one-way ANOVA revealed a significant group effect, $F_{(2,\ 51)} = 7.8$, $p = .001$, $\eta_p^2 = 0.23$, which a post hoc comparison confirmed was due to a smaller aftereffect in *magnitude only* participants relative to *magnitude plus direction* ($p = .001$, $\alpha = 1.4$) and *direction only* ($p = .01$, $\alpha = 0.9$; Bonferroni corrected) participants. As in Experiments 2 through 4, despite all three groups adjusting their heading angles to compensate for the presence of the visuomotor rotation, a sizable aftereffect was only present in participants who received direction feedback through

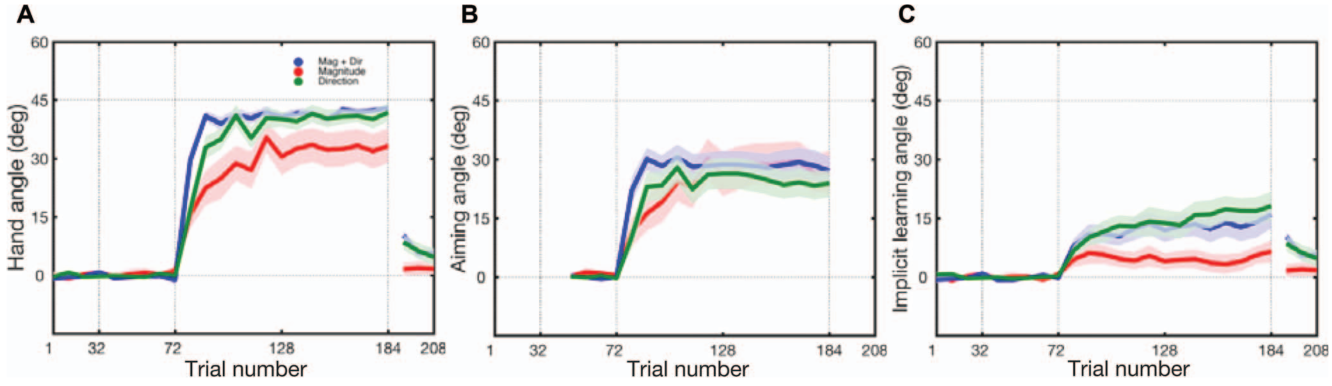

Figure 7. Experiment 5: Single target with verbal aim reports performance metrics. (A) Hand heading angle, (B) aim reports, and (C) implicit learning estimate (Hand Angle – Aim) for *magnitude plus direction* (blue), *magnitude only* (red), and *direction only* (green) feedback groups. For visualization purposes, trials were binned by eight trials (a full cycle of all targets) for each participant, the mean (solid line) and standard error (shaded region) are then plotted for each group.

either *direction only* feedback or *magnitude plus direction* feedback, with no reliable aftereffect found in participants who received *magnitude only* feedback. Our focus in Experiment 5, however, was accessing explicit aiming strategies and implicit adaptation during the rotation block using verbal aim reports.

Verbal reports. The time course of explicit aiming data reveals that, as predicted, for participants in all three groups, a large portion of the heading angle change was due to explicit aiming (Figure 7B). All three groups had an initial shift in aiming location during the first eight trials of the rotation block (*magnitude plus direction*: 22.0 ± 3.4°; *direction only*: 10.2 ± 3.3°; *magnitude only*: 11.4 ± 3.7°) and further shifted their aim by the end of the rotation block (*magnitude plus direction*: 27.1 ± 3.6°; *direction only*: 23.8 ± 3.6°; *magnitude only*: 26.8 ± 5.2°). A repeated measures ANOVA revealed a main effect of time, $F_{(1,\,51)} = 32.4$, $p < .0001$, $\eta_p^2 = 0.39$, was present as aiming angle increased from early to late in the rotation. Although no main effect of group, $F_{(2,\,51)} = 1.3$, $p = .29$, $\eta_p^2 = 0.05$, was present, a trend was present for a Group × Time interaction, $F_{(2,\,51)} = 2.5$, $p = .09$, $\eta_p^2 = 0.09$. Although participants who received *magnitude plus direction* feedback appeared to have a larger shift in aim early in the rotation block, all three groups had shifted a similar amount by the end of the block.

Implicit learning was estimated by subtracting the reported aiming angle from the heading angle for each participant on each trial (Figure 7C), with statistical analysis focused on the first and last eight trials of the rotation block. In the rotation block, the groups with direction feedback had an implicit learning estimate that increased from early (*magnitude plus direction*: 7.8 ± 1.9°; *direction only*: 6.7 ± 1.6°) to late in the block (*magnitude plus direction*: 15.9 ± 3.5°; *direction only*: 18.1 ± 3.7°). Consistent with the lack of an aftereffect in the *magnitude only* group, the implicit learning estimate was very small both early (magnitude only: 4.5 ± 1.9°) and late (magnitude only: 6.5 ± 2.8°) in the rotation block. A repeated-measures ANOVA found a main effect of time, $F_{(1,\,51)} = 19.4$, $p < .0001$, $\eta_p^2 = 0.28$, indicating that overall implicit learning increased from early to late in the rotation block. A trend for a main effect of group, $F_{(2,\,51)} = 2.9$, $p = .07$, $\eta_p^2 = 0.10$, and a Group × Time interaction, $F_{(2,\,51)} = 2.8$, $p = .07$, $\eta_p^2 = 0.10$, were also present. Our main comparison of interest was the implicit learning estimate between *magnitude only* and *direction only* participants. A *t* test comparing the late rotation phase for the two groups confirmed the implicit learning estimate was significantly smaller for *magnitude only* participants ($t_{34} = 2.5$, $p = .02$, $\alpha = 0.8$) relative to *direction only* participants.

In summary, receiving direction information through either combined magnitude and direction feedback, or through isolated direction feedback results in sensorimotor adaptation. This is true when sensorimotor adaptation is measured by an implicit learning estimate over the course of the rotation block, or an aftereffect during washout. Although isolated magnitude feedback allowed participants to counter the rotation through the use of an explicit aiming strategy, it did not result in sensorimotor adaptation.

General Discussion

Decomposition of Error-Based Feedback

Task-based feedback has long been known to be important for learning (Adams, 1987; Trowbridge & Cason, 1932). In the case of learning to counter a visuomotor rotation, sensorimotor adaptation (i.e., aftereffects) appears to be highly dependent on the presence of a visuospatial error signal. When feedback is indirectly provided in the form of symbolic markers of task success, the sensorimotor map fails to update (Brudner et al., 2016; Izawa et al., 2011; Nikooyan & Ahmed, 2015). To determine what direct feedback gives rise to adaptation, we decomposed the visuospatial form of the error into its constituent components: direction and magnitude feedback. Adaptation was present when the visuospatial feedback conveyed direction information. In contrast, adaptation was minimal or absent when only the magnitude component of feedback was provided.

When error feedback is present, individual learning curves likely reflect the combination of changes in action selection (i.e., aiming) and the adaptation of a forward model. The amount of information appears to tip the balance between these two processes. When cursor feedback is minimal, learning is mainly composed of changes in action selection, however, when the amount of cursor feedback is sufficient to induce adaptation, the contribution of action selection to learning is reduced (Taylor et al., 2014; Izawa & Shadmehr, 2011; Peled & Karniel, 2012). The forms of learning present in the two processes appear quite different. Aim reports (exp. 5) show exploratory behavior, with abrupt changes in either direction (see also Taylor et al., 2014). In contrast, the implicit learning function looks more similar to the slow, monotonic updating of an internal model, which is considered a hallmark of adaptation (Huberdeau et al., 2015). In Experiment 5, we found that when feedback contained information about the direction of the error, learning, in this case changes in heading angle, occurred through both changes in aiming location and internal model adaptation. However, when feedback was limited to error magnitude, changes in heading angle were more attributable to changes in aiming location.

How does a small, distinct cursor, looking nothing like a human effector, induce sensorimotor adaptation? Although it might seem that the motor system can use feedback from any visual stimulus that correlates with movement, this does not appear to be entirely the case. In Experiments 2 through 5, we show that adaptation is small or negligible when direct feedback is limited to only magnitude information. In the *magnitude only* online feedback condition the feedback line has a fixed direction, whereas the length of the line represents the distance of the cursor from the target. Consequently, if a participant makes a correct reach that guides the cursor directly to the target, visual movement will be correlated with hand movement. This contrasts with the *direction only* condition, which was found to consistently lead to adaptation. In the *direction only* feedback condition the line was of a fixed length, but would point to the unseen cursor relative to the target. With this feedback, if a participant made a movement that would take the cursor directly to the target, the line would continue pointing toward the start position until the target was hit, resulting in very little, if any, movement of the visual feedback. Thus, the degree of spatiotemporal correlation between limb and cursor movement does not appear to correlate with adaptation magnitude.

Although it may seem surprising that magnitude information does not affect the amount of adaptation, recent work has supported the idea that adaptation is more stereotyped across tasks than previously thought (Fine & Thoroughman, 2006; Wei & Körding, 2009). When perturbations are infrequent and randomly presented, single-trial adaptation is the same, regardless of the size and timing of perturbations (Fine & Thoroughman, 2006), or whether the perturbation is a visuomotor rotation or a force field (Wei & Körding, 2009). Proportional responses reappeared only when the perturbations became more consistent (Fine & Thoroughman, 2007). However, in Bond and Taylor (2015), the rotations were always consistent, but the amount of adaptation did not depend on visuomotor rotation size. Despite varying rotation sizes being given across participants, adaptation never exceeded more than ~15°, even when a 90° rotation was implemented. The similar saturation of adaptation across rotation sizes in Bond and Taylor (2015) is parsimoniously explained by our current results, which suggests that error magnitude information is not what leads to the change in adaptation but rather the error direction information. At rotation sizes above 15° any additional changes in hand angle were the result of the use of an explicit aiming strategy (Bond & Taylor, 2015). Although highly speculative, it is possible that the return of proportionality seen in Fine and Thoroughman (2007) is due to more consistent perturbations allowing for the addition of an aiming solution. Additionally, sensitivity may manifest if the perturbations are sufficiently small and fall within the natural distribution of errors (Wei & Körding, 2009; Marko et al., 2012).

One alternative explanation for the lack of sensitivity to the magnitude of the error, is that, by definition, a rotational perturbation induces directional errors. These errors would only affect the direction of movement and not the extent of the movement, which appear to be distinct components of motor planning (Gordon et al., 1994). If instead we manipulated the gain between the cursor and hand, then we would observe sensitivity to the magnitude of the gain and insensitivity to the direction of the error produced by the gain. However, this explanation conflates planning of the radial extent of a movement and the magnitude of an error. A magnitude and direction component is present in both gain and rotation manipulations. That is, regardless of the direction of a rotational perturbation, the rotation size is critical—a 15° rotation should lead to 15° of adaptation, whereas a 60° rotation should lead to 60° of adaptation. Likewise, for gain change, the motor system would still need to know whether the gain was increased or decreased and by how much. Thus, this geometrical relevancy argument for the lack of sensitivity to error magnitude cannot explain the results presented here.

A second alternative explanation is that differences in attentional saliency between the *direction only* and *magnitude only* groups may account for the differences reported in adaptation. One could argue that the *direction only* feedback is the least salient, as the feedback is relatively constant throughout the movement, while the length of the line will change continuously along with the hand approaching the target for both *magnitude only* and *magnitude plus direction* feedback conditions. Additionally, the feedback was likely the most salient for the *magnitude plus direction* group, as both the direction and magnitude of the line changed along with movement of the hand. Thus, the lack of a consistent difference in adaptation between the *magnitude plus direction* and *direction only* groups suggests feedback saliency was not a factor.

Importantly, a lack of sensitivity to the magnitude of an error is also present when force fields are used as the perturbation (Fine & Thoroughman, 2006), suggesting it is not just the saliency of the visual error that results in this lack of sensitivity. Additionally, there are reasons to think that attentional saliency does not affect implicit learning. Rand and Rentsch (2015) manipulated the gaze location of participants while learning a visuomotor rotation task: One group was told to hold their gaze on the primary target, a second group was told to hold their gaze on where they were aiming, and a third group was allowed to freely change their gaze. Implicit adaptation was found to be unaffected by gaze location, suggesting that location of fixation and, perhaps, attentional saliency of an error does not affect adaptation. Additionally, adaptation has been shown to proceed when it is irrelevant to task goals (Morehead et al., in press; Schaefer et al., 2012) or even when counter to task goals in the case of drift (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011). As we would expect attentional saliency to change in response to task goals, this further suggests that attentional saliency may play little role in implicit adaptation.

Theoretical Implications

An internal forward model is thought to predict the sensory consequences of an action, allowing for rapid adjustments in behavior, before the action is even complete (Wolpert & Kawato, 1998; Wolpert & Miall, 1996). To function in a constantly changing environment these forward models need to be updated when an error is present, a process known as *adaptation* (Krakauer et al., 1999). A forward model is thought to be updated due to the presence of a sensory prediction error, a mismatch between the actual and predicted sensory consequences of a movement (Tseng et al., 2007). One proposal is that the update to the forward model is driven by the actual feedback correction (Albert & Shadmehr, 2016). This would lead to the possibility that the differences in adaptation observed between *magnitude only* and *direction only* groups may be due to differences in the feedback corrections being made in response to the feedback. However, this explanation is unlikely, as the *direction only* group had very similar performance to the *magnitude plus direction* group, despite the differences in feedback likely leading to different feedback corrections between those groups as well. Further, in Experiment 4, we demonstrate that the differences in adaptation are not due to differences in the feedback corrections between groups. Additionally, the time to target was similar for all three groups in Experiment 3, suggesting there was not a substantial difference in the number of corrections made between the groups. These results are also in agreement with previous studies demonstrating visuomotor adaptation when feedback corrections are restricted (Tseng et al., 2007; Wallman & Fuchs, 1998).

The unique neural circuitry of the cerebellum has led many to suggest that it plays a critical role in error-driven updates to a forward model (Ito, 2000). These theories are supported by evidence that cerebellar pathology is linked to impairments in a range of sensorimotor adaptation tasks (Martin et al., 1996a; Rabe et al., 2009; Schlerf et al., 2013; Smith & Shadmehr, 2005; Weiner et al., 1983). In visuomotor rotation tasks, individuals with cerebellar pathology exhibit a reduced ability to counter perturbations, as well as attenuated aftereffects when the perturbation is removed (Schlerf et al., 2013; Werner et al., 2009). The role of the cerebellum in maintaining an effective forward model is further supported by neuroimaging studies in humans (Krakauer et al., 2004; Miall et al., 2001; Schlerf et al., 2012), and neurophysiological studies in nonhuman species (Horn et al., 2004; Medina et al., 2000), which show that cerebellar activity is correlated with sensory prediction errors.

Though no data exists regarding a lack of magnitude response in the cerebellum in human participants, a study of saccadic adaptation in nonhuman primates showed that purkinje cells in the vermis of the oculomotor cerebellum responded categorically to error, such that complex spike activity responded to only the direction of the eye position error, but not the magnitude (Soetedjo & Fuchs, 2006). Neurophysiologists have struggled to understand how the seemingly on/off nature of complex spikes in the cerebellum could encode magnitude information. Although some have suggested the temporal synchrony of complex spikes may code for magnitude of an error (Najafi & Medina, 2013), this model still only allows for a few graded levels of magnitude.

Critically, computational models of sensorimotor adaptation have focused on a learning rate that is a function of the size of the error committed (Jordan & Rumelhart, 1992; Thoroughman & Shadmehr, 1999). Accordingly, these models predict the adjustment in a forward model is proportional to the magnitude of the preceding error (Abeele & Bock, 2001). In contrast, we have shown that forward model adaptation is a result of the direction of the error, rather than its magnitude. Thus, models of adaptation should only incorporate information about the direction of an error. Although one can develop models that effectively operate on an isolated direction signal, such as using RPROP gradient descent (Herzfeld et al., 2014) or causal relevance modulation (Wei & Körding, 2009), these models would need to provide a mechanistic explanation that can align with neurophysiological data. Alternatively, sensitivity to error magnitude may be more useful in modeling the formation of higher-level action selection (i.e., aiming), drawing inspiration from the work in the reinforcement learning and decision-making communities.

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