Understanding implicit sensorimotor adaptation as a process of kinesthetic re-alignment

By

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Abstract

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From elementary skills such as walking and talking, to complex ones such as playing tennis or music, humans are remarkably adept at learning to use their bodies in a coordinated manner. However, these abilities can be fragile: Many neurological conditions can compromise motor performance and learning. Understanding how the brain produces skilled movement will not only elucidate principles of learning but can also optimize rehabilitation interventions for individuals with movement disorders.

Motor learning is not a unitary operation but relies on multiple learning processes (Kim, Avraham, and Ivry 2020; Krakauer et al. 2019). For example, reinforcement learning helps us select rewarding actions (Dayan and Daw 2008), use-dependent learning helps us rapidly execute well-practiced actions (Verstynen and Sabes 2011; Classen et al. 1998), and sensorimotor adaptation keeps our movements well-calibrated in response to changes in the body and environment (Helmholtz 1924; Stratton 1896). In addition, recent work has highlighted how these implicit processes may be complemented by explicit processes (Codol, Holland, and Galea 2018; Collins and Frank 2012; Marinovic et al. 2017; Jonathan S. Tsay, Kim, Saxena, et al. 2022). For example, when asked to move in a novel environment in which the visual feedback is altered (e.g., prism glasses), participants may adopt a re-aiming strategy to nullify the perturbation. Unlike implicit forms of learning, explicit processes allow for rapid changes in performance (Kim, Avraham, and Ivry 2020; Krakauer et al. 2019; Inoue et al. 2015; Smith, Ghazizadeh, and Shadmehr 2006; Schween et al. 2020; Daniel M. Wolpert and Flanagan 2016; Facchin et al. 2019).

The joint operation of multiple learning processes has made it difficult to characterize features inherent to each process. To address this, new analytical methods have been recently developed to isolate individual components (Brudner et al. 2016; Jonathan S. Tsay, Haith, Ivry, et al. 2022; Marinovic et al. 2017; Yang, Cowan, and Haith 2021), providing new opportunities to revisit classic problems in sensorimotor learning: What is the critical signal driving learning for different processes? Are there limits to plasticity, and does this vary between processes? How does the quality of sensory feedback impact different components of motor learning?

I exploit these methods in this dissertation to revisit the mechanisms at play in sensorimotor adaptation. Implicit adaptation has been framed as an iterative process designed to minimize sensory prediction error, the mismatch between a desired and experienced sensory outcome (Donchin, Francis, and Shadmehr 2003; R. Morehead and Smith 2017; Albert et al. 2022, 2021; Herzfeld et al. 2014; Kim et al. 2018; Thoroughman and Shadmehr 2000). Traditionally, the focus has been on how *visual* sensory prediction errors are used to modify a visuomotor map, ensuring that future movements are more accurate. According to this visuo-centric view, the upper bound of implicit adaptation represents a point of equilibrium, one at which the trial-by-trial change in hand

position in response to a visual error is counterbalanced by a trial-by-trial decay ('forgetting') of this modified visuomotor map back to its baseline, default state.

Despite its appeal, the visuo-centric view is an oversimplification. The brain exploits information from all of our senses, not only from vision (Ernst and Banks 2002; Van Beers, Sittig, and Gon 1999; Chancel, Ehrsson, and Ma 2022; Sober and Sabes 2005, 2003). This insight, paired with the empirical data outlined in this dissertation, have inspired a new, 'kinesthetic re-alignment' model of implicit adaptation (Jonathan S. Tsay, Kim, Haith, et al. 2022). By this view, implicit adaptation is an iterative process designed to minimize a 'kinesthetic' sensory prediction error, the misalignment between the perceived heading angle and the movement goal. The perceived hand position is a composite signal, reflecting the seen hand position (via visual afferents), the felt hand position (via peripheral proprioceptive afferents based on mechanoreceptors from muscles, joints, and skin), the predicted hand position (via the efferent motor command), and the movement goal (via a prior belief that the movement will be successful). Implicit adaptation will cease when the kinesthetic error is nullified, that is, when the perceived hand position and the movement goal are re-aligned. (Footnote: Whereas we had used 'proprioception' in our published work featured in this dissertation, we will adopt the term "kinesthesia" here in the Abstract given that the perceived hand is a composite kinesthetic representation that encompasses both central beliefs and peripheral senses (Proske and Gandevia 2012)).

In Chapter 1, I tested a core assumption held by studies of implicit sensorimotor adaptation, namely that the perceived hand position is at the target (subject to random noise). Specifically, we used a novel visuomotor task that isolated implicit adaptation and probed kinesthesia in a fine-grain manner (i.e., the participant's perceived heading position on each trial). Whereas participants exhibited robust implicit adaptation (i.e., changes in hand position away from the target in the opposite direction of the visual error), their perceived hand position remained near the target. However, to our surprise, the position reports exhibited a non-monotonic function over the course of adaptation: The participants initially perceived their hand to be biased towards the perturbed visual feedback, mis-aligned with the movement goal. However, over time the reports shifted away from the perturbed visual feedback, re-aligning back to the target. Together, these data not only revealed unappreciated kinesthetic changes that arise during learning but also seeded the idea for a kinesthetic re-alignment perspective of implicit adaptation.

In Chapter 2, I evaluate whether there is a relationship between kinesthetic perception and implicit adaptation, one that would not be predicted by visuocentric models. By using two visuomotor tasks that isolated implicit adaptation and probed kinesthesia, we discovered that participants who have greater kinesthetic biases towards the perturbed visual feedback and greater baseline kinesthetic uncertainty exhibited greater implicit adaptation. As such, these data provided evidence for new, unexplained kinesthetic constraints on the extent of implicit adaptation, supporting the notion that kinesthetic perception plays a critical role in implicit adaptation.

The empirical results from the previous chapters led us to develop a new, kinesthetic re-alignment model of implicit adaptation. I will formalize this model in Chapter 3, demonstrating how it readily explains the non-monotonic time course of perceived hand position during implicit adaptation (Chapter 1 and the relationship between kinesthetic biases/uncertainty with the extent of implicit adaptation (Chapter 2). Moreover, I will demonstrate how the kinesthetic re-alignment model is also able to capture a myriad of observations not accounted for by a visuo-centric view of adaptation. Taken together, the kinesthetic re-alignment model brings us one step closer to a more holistic view of motor adaptation, a perspective that formalizes how our high-level beliefs and low-level senses inform where we are positioned and how we are to adapt.

Table of contents

List of figures

To my dearest, Sophia.

Acknowledgments

To my Ph.D. advisor, Rich:

“You let me make a difference.”— Alexander Hamilton

To my committee members, Anne and Emily:

“There is a million things I haven’t done, just you wait.” —Alexander Hamilton

To my friends and labmates:

“We'll tell the story of tonight." —Alexander Hamilton, John Laurens, Hercules Mulligan, and Marquis de Lafayette

To my research assistants:

“If we lay a strong enough foundation. We'll pass it on to you, we'll give the world to you.” — Alexander Hamilton

To my parents:

I love you.

Chapter 1: Continuous reports of sensed hand position during implicit sensorimotor adaptation

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In this Chapter, I tested a core assumption held by studies of implicit sensorimotor adaptation, namely that the perceived hand position is at the target: Sensorimotor learning is thought to entail multiple learning processes, some volitional and others automatic. A new method to isolate implicit learning involves the use of a "clamped" visual perturbation in which, during a reaching movement, visual feedback is limited to a cursor that follows an invariant trajectory, offset from the target by a fixed angle. Despite full awareness that the cursor movement is not contingent on their behavior, as well as explicit instructions to ignore the cursor, systematic changes in motor behavior are observed, and these changes have the signatures of motor adaptation observed in studies using classic visuomotor perturbations. While it is clear that the response to clamped feedback occurs automatically, it remains unknown if participants are sensitive to the large deviations in hand position that occur during adaptation. To address this question, we used the clamp method and asked participants to report their hand position after each reach. As expected, we observed robust deviations in hand angle away from the target (average of ~18°). The hand reports also showed systematic deviations over the course of adaptation, initially attracted towards the visual feedback and then in the opposite direction, paralleling the shift in hand position. However, the shift in perceived hand position was subtle, reaching only ~2° at asymptote. These results confirm that participants have limited awareness of the behavioral changes that occur during sensorimotor adaptation, while revealing the impact of feedforward and feedback signals on their subjective experience.

Introduction

Motor adaptation is the process of calibrating well-practiced actions to maintain performance in response to changes in the environment or body. A large body of work has focused on how sensory prediction error, the difference between predicted and actual sensory feedback, drives motor adaptation in an automatic manner (Shadmehr, Smith, and Krakauer 2010). For instance, if a fatigued ping-pong player begins to produce shots that land close to the net instead of the opponent's back line, her motor commands would be re-calibrated to result in more forceful movements.

Perturbations of the visual feedback have offered one approach to study motor adaptation in the laboratory (Krakauer et al. 2000; Helmholtz 1924; Gordon M. Redding, Rossetti, and Wallace 2005). In visuomotor rotation tasks (Krakauer et al. 2000), participants are initially trained to reach to visually defined targets, with veridical feedback of their hand position represented by a cursor. Following this baseline period, a rotation is imposed between the position of the hand and the position of the cursor. To counteract the rotation, the motor system must adjust future movements, generating commands that lead to hand movements in the opposite direction of the perturbation.

While the participant's phenomenological experience *after* learning suggest that the change in behavior is largely implicit (at least for rotations up to 45°), recent methods using probes continuously *during* learning (e.g., aim reports) have made clear that standard visuomotor rotation tasks elicit multiple learning processes (Taylor and Ivry 2011; Bond and Taylor 2015; Mazzoni and Krakauer 2006; Taylor, Krakauer, and Ivry 2014; Shmuelof et al. 2012). These standard visuomotor tasks conflate sensory prediction errors with task performance errors: The former is assumed to be the driving force for automatic adaptation, whereas the latter has been shown to elicit voluntary strategic changes in performance (Werner et al. 2015; Taylor, Krakauer, and Ivry 2014). Thus, explicit changes in action selection operate in parallel with implicit changes occurring within the motor execution system.

To study sensorimotor adaptation in the absence of strategy use, Morehead et al. (2017) introduced a "visual error clamp" method. As with standard visuomotor rotation tasks, participants reach to a visual target, with feedback limited to a cursor that is time-locked to the radial distance of the hand from the starting position. However, with the clamp method, the cursor follows an invariant path, always offset from the target by a fixed angle. Thus, unlike standard adaptation tasks, the angular position of the feedback is not contingent on the participant's behavior. Despite being fully informed of the manipulation and instructed to always reach directly to the target, the participant's behavior exhibit all of the hallmarks of adaptation, with the heading angle gradually shifting in the direction opposite to the clamped feedback. Presumably, this change is driven because the adaptation system, in an obligatory manner, treats the discrepancy between the target and feedback cursor as a sensory prediction error. Since the "error" never changes, the learning function can be observed in the absence of other sources concerning performance (e.g., the reduction in task error that occurs in standard adaptation tasks). Quite strikingly, the change in heading angle will continue for a few hundred trials, reaching asymptotic values that average around 20°, and even reach values greater than 45° in some participants (Kim et al. 2018).

If the visual error clamp elicits motor adaptation in an automatic manner, we might expect participants to be unaware of the resulting change in behavior. The presence of a persistent aftereffect once the clamped perturbation is removed indicates that participants are unaware of the (often substantial) adaptive changes in the sensorimotor map. This hypothesis is in accord with the participants' subjective reports: When queried at the end of the experimental session, participants generally report that they had followed the instructions, reaching directly to the target throughout the experiment.

Here we took an alternative approach to these indirect or retrospective probes on awareness, asking participants to report their hand position *after* each reach over the course of adaptation. If participants are unaware of their adapted behavior, then the reported hand positions should remain at the target location, with perhaps some variation due to motor and perceptual noise. Alternatively, participants may respond to the clamped error in an obligatory manner but also be aware of the resulting change in behavior. In the extreme, the hand reports would track the true hand position. Such an outcome would be reminiscent of the alien hand sign (Brion and Jedynak 1972), a condition in which patients are aware that they are producing "unintended" movements, but cannot volitionally control these movements.

Methods

Young adults (n = 32, 21 female, mean age = 21, age range: 18 - 25) were recruited from the Berkeley community. All participants were right-handed, as verified with the Edinburgh Handedness Inventory (Oldfield 1971). Participants received course credit or financial compensation for their participation. The protocol was approved by the institutional review board at the University of California, Berkeley.

We did not perform a power analysis to predetermine our sample size. Our experiment used a novel hand report technique to probe participants' sensed hand position during adaptation, and thus, there are no data to guide our expectations regarding possible changes in perceived hand position. The closest guide here would be the post-experiment surveys and these data are usually reported in a qualitative manner, simply indicating that participants were unaware of the changes in hand position during adaptation. Instead, the sample sizes were based on our previous work with the clamp method (Kim et al. 2018; R. Morehead et al. 2017), assessing our sensitivity to detect changes in hand angle in response to clamped feedback. With a sample size of 16 in each experiment and criteria of 80% power and alpha < 0.05, we have sufficient statistical power to detect moderate effect sizes in changes in actual hand position (smallest detectable Cohen's $d_z = 0.65$, calculated using G*power software (Faul et al. 2007, 2009).

Reaching Task

Participants were seated at a custom-made table (Figure 1.1a) that housed an LCD screen (53.2 cm by 30 cm, ASUS) mounted 27 cm above a digitizing tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA). The participant made reaching movements by sliding a modified air hockey "paddle" that contained an embedded stylus. The tablet recorded the position of the stylus at 200 Hz. The experimental software was custom written in Matlab, using the Psychtoolbox extension (Brainard 1997).

On each trial, the participants made a center-out planar reaching movement from the center of the workspace to a visual target. The center position was indicated by a white circle (0.6 cm in diameter) and the target location was indicated by a blue circle (also 0.6 cm). The target could appear at one of four locations on an invisible virtual circle (45°, 135°, 225°, 315°), with a radial distance of 8 cm from the start location. The monitor occluded direct vision of the hand, and peripheral vision of the arm was minimized since the room lights were extinguished during the experimental session.

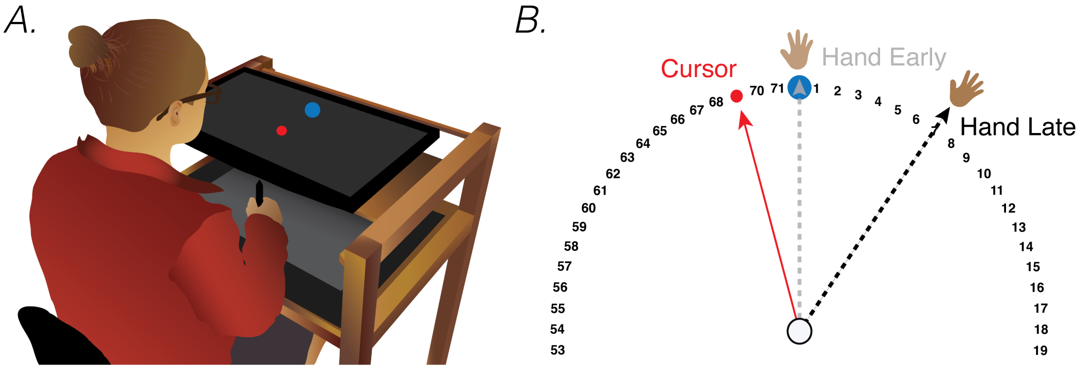

Figure 1.1. Experimental Methods. **A)** Experimental apparatus and setup. **B)** Schematic overview of the error clamp paradigm, in which the angular path of the cursor is held constant, and independent of hand movement direction. Dotted lines depict representative trajectories at the start (Early) and end (Late) of the error clamp block.

To initiate each trial, the participant moved the stylus into the start location. Feedback of the position of the hand, given in the form of a white cursor (0.35 cm diameter), was only provided when the stylus was within 2 cm of the center of the start circle. Once the participant moved the stylus into the start circle and maintained that position for 500 ms, the target appeared. The location of the target was selected in a pseudo-randomized manner, with each location sampled once every four trials. The participant was instructed to reach, attempting to rapidly "slice" through the target. The feedback cursor, when presented (see below) remained visible throughout the duration of the reach and remained fixed for 500 ms at the endpoint location when the movement amplitude reached 8 cm. If the movement was not completed within 300 ms, the message "too slow" was played over the speaker.

The feedback could take one of three forms: veridical feedback, no-feedback, and error clamp feedback. During veridical feedback trials, the location of the visual feedback was veridical, corresponding to the location of the stylus/hand. During no-feedback trials, the feedback cursor was extinguished as soon as the stylus left the start circle and remained off for the entire reach. The cursor only became visible during the return phase of the trial when the stylus was within 2 cm of the start circle. During error clamp trials (Figure 1.1b), the cursor moved along a fixed trajectory relative to the position of the target. The clamp was temporally contingent on the participant's movement, matching the radial distance of the stylus from the center circle (up to 8 cm), but non-contingent on the movement in terms of its angular offset. The fixed angular offset (with respect to the target) was 15° in Experiment 1 and 45° in Experiment 2. The participant was instructed to "ignore the visual feedback and reach directly to the target."

On some trials, the participants were required to provide a hand report. For these trials, the participant was instructed to maintain their hand position at the end of the outbound segment. A series of numbers appeared as soon as the amplitude of the movement exceeded 8 cm, separated by 5° to form a virtual ring at a radial distance of 8 cm. The numbers ("0" to "71") ascended in the clockwise direction, with the number "0" positioned at the target location. The participant reported their hand position by verbally indicating the number closest to the perceived location of the stylus.

Experiment 1:

To probe awareness of the consequences of motor adaptation, the participants (n=16) in Experiment 1 were asked to report their hand position after each reaching movement. The experiment was organized into six blocks of trials. The first three blocks assessed baseline performance in the absence of a perturbation. The first block was composed of 20 reach-only trials without feedback to familiarize the participants with the apparatus (cycles 1 – 5, with each cycle consisting of one reach to each of the four targets). After this block, the hand report procedure was introduced and was included in the remaining five blocks (trials 21 — 360). These consisted of 40 trials with veridical feedback (cycles 6 – 15), 40 more trials without feedback (cycles 16 – 25), 200 trials with error clamp feedback (cycles 26 – 75), 40 trials with no feedback (aftereffect, cycles 76 – 85), and a final set of 20 trials with veridical feedback (washout, cycles 86 – 90). During the error clamp block, the cursor always followed an invariant trajectory, displaced from the target by 15°. The direction of this displacement was either clockwise or counterclockwise, counterbalanced across participants. Note that we sandwiched the error clamp block with no feedback blocks to provide a measure of adaptation that accounts for idiosyncratic biases in reaching.

Before the error clamp block, the experimenter provided instructions describing the error clamp, emphasizing that its angular trajectory was independent of the participant's movement and thus, should be ignored. To reinforce the uncoupling of the movement and feedback, three demonstration trials were presented. On the first trial, a target appeared at the 90° location (straight ahead), and the experimenter instructed the participant to first "Reach straight to the left" (i.e., 180°). During the reach, the cursor moved along a trajectory displaced 15° away from the target (matching the direction to be employed with that participant). For the second and third demonstration trials, the target again appeared at 90°, and the participant was instructed to "Reach straight to the right" (0°) and "Reach backward towards your torso" (270°), respectively. For these trials, the cursor again followed a trajectory displaced 15° from the target. After confirming that the participant understood the nature of the feedback, the experimenter again emphasized that the participant should always reach directly to the target and ignore the feedback. The participant then completed the 200-trial block with clamped feedback. Before the 40-trial aftereffect block, the participant was told that no feedback would be provided and that they should continue reaching directly to the target. Prior to the final washout block, the participant was told that the feedback would now correspond to the position of the stylus, and again instructed to reach directly to the target.

Experiment 2:

We repeated the basic hand task in Experiment 2 with a few notable changes. The size of the error clamp was increased to 45° to increase the spacing between the target and the terminal position of the cursor on clamped feedback trials. This manipulation was included to minimize the possibility that, in making their post-reach reports, the participant might confuse the positions of the target and cursor, potentially biasing their reports. Moreover, an intermittent method introduces gaps in the report data and, as such, would reduce the effects of memory on reports, at least at the start of a new hand report mini-block. An intermittent method may also make participants attend more to their hand reports if these were limited to selected trials, potentially discouraging any habitual response patterns.

Most importantly, a second error clamp block was added immediately after the first error clamp block in which the direction of the clamp was reversed: If the first clamp block involved a clockwise rotation, the second clamp block involved a counterclockwise rotation, and vice-versa. We expected the hand angle direction would reverse in response to the new clamp, eventually leading to movements in the opposite direction of the reversed clamp. In this manner, we expected to greatly increase the range of changes in hand angle over the course of the experiment. We could exploit this increased range in hand angle to probe whether the hand reports also demonstrate a reversal in direction and increase in range.

Each participant completed 6 blocks: No feedback baseline (cycles 1 – 5: 20 trials), veridical feedback with hand report (cycles 6 – 15: 40 trials), no feedback with hand report (cycles 16 – 25: 40 trials), initial error clamp (cycles 26 – 75: 180 trials), reversed error clamp (cycles 71 – 135: 260 trials), and a final washout block with veridical feedback (cycles 136 – 140: 20 trials). Based on the results of Experiment 1, we reduced the number of trials in the first clamp block to 180, anticipating that participants would be near asymptotic performance. The number of trials in the second clamp block was extended to 260 trials to allow the reversed clamp to first bring the hand angle back towards the target and then reach asymptotic performance in the opposite direction. In this manner, we expected to maximize the range of hand angles, (i.e., essentially double the range over Experiment 1). We did not include a no-feedback aftereffect block given that the results of Experiment 1 showed that the relationship between hand position and hand reports was maintained when the clamped feedback was removed. We opted to conclude the session with a feedback washout block to ensure that participant's hand reports remained consistent with their awareness of hand position (i.e., overlapping hand report and hand angle functions).

The hand report procedure lengthens the interval between successive reaches (i.e., time spent reporting the sensed hand location and finding the center position to initiate the next reach). The time interval following successive reaches with hand reports averaged 842 ms longer than the interval following trials without hand reports (hand reports: 3577 ms, without hand reports: 2735 ms). Given that the magnitude of implicit adaptation exhibits a time-dependent decay (Hadjiosif et al. 2014) and our desire to maximize the range of hand angles, we opted to use an intermittent procedure to sample the hand reports. These hand reports were collected in 10 mini-blocks, interspersed across the different reach blocks of the experiment: cycles 6 – 15 (veridical feedback), 16 – 25 (no feedback), 26 – 30 (clamp feedback), 46 – 50 (clamp feedback), 66 – 70 (clamp feedback), 71 – 75 (reversed clamp feedback), 91 – 95 (reversed clamp feedback), 111 – 115 (reversed clamp feedback), 113 – 135 (reversed clamp feedback), and 136 – 140 (veridical feedback washout).

Finally, we modified the procedure used to demonstrate the lack of contingency between the direction of the hand movement and trajectory of the feedback cursor. For the three demonstration trials presented just before the first error clamp block, the target always appeared at the 180° target, and the participant was told to "Reach straight for the target". Across trials, the feedback cursor terminated at 90° (first trial), 270° (second trial), and 0° (third trial) locations. Following the last demonstration trial, verbal confirmation was obtained that the participant understood that the direction of the cursor was not under his or her control. The experimenter then informed the participant that the cursor feedback would now move in an invariant direction and reinforced the instructions that the participant should ignore the cursor.

There was a mandatory one-minute break between the first error clamp block and the reverse error clamp block. During this break, the experimenter informed participants that the cursor feedback will now follow an invariant trajectory in the opposite direction. Before proceeding, the experimenter obtained verbal confirmation that the participant again understood that the cursor feedback was not tied to his or her movement and should be ignored in its entirety. The participant then completed the 260-trial block with the reverse clamped feedback. Before the last washout block, the experimenter reminded participants to continue reaching directly to the target, with feedback reflecting his or her hand position in a veridical manner.

Baseline subtraction

The primary dependent variable of reach performance was the hand angle relative to the target, measured at the peak velocity. Outlier responses were defined as trials in which the hand angle was greater than 90° from the target location. These were removed from the analysis and constituted only 8 trials out of a total set of 5760 trials.

The hand angle data were pooled over a movement cycle, defined as four consecutive reaches, one to each of the four targets. For each cycle, the means were baseline corrected on an individual basis to account for idiosyncratic angular biases in reaching to the four target locations. These biases were estimated based on heading angles during the last three no feedback baseline cycles (Experiments 1 and 2: cycles 23 – 25), with these bias measures then subtracted from the data for each cycle. For visualization purposes, the hand angles were flipped for blocks in which the clamp was counterclockwise with respect to the target.

The hand report data were converted into angular values, although we note that the reports involve categorical data (numbers spaced at 5° intervals), whereas in angular form they suggest a continuous variable. The hand report data were also baseline corrected on an individual basis to account for idiosyncratic report biases to the four target locations in the exact manner the hand angle data were pre-processed.

Cluster Permutation Analysis

To evaluate whether participants in Experiment 1 systematically adapted to the visual error clamp, we used a cluster permutation analysis that consisted of two steps. First, a paired t-test was performed for each cycle (after the baseline blocks), asking if the observed hand angle diverged from the hand angle during baseline reaches (cycles 6 to 25). Clusters were defined as epochs of two or more cycles in which t-values exceeded a threshold of a p-value less than 0.05. The t-values were then summed within each cluster to obtain a cluster t-score. Second, we compared the observed t-scores to the distribution of the maximum absolute t-scores (a control for multiple comparisons to limit type-I error rates (Nichols and Holmes 2002)) obtained by repeating step 1 on the shuffled data, which was created by randomly assigning condition labels (baseline or observed hand angle) 1000 times. A p-value is obtained by evaluating the proportion of random permutations with t-scores greater than the observed t-score.

The cluster permutation analysis was also used for two analyses relevant to the hand report data. First, a cluster analysis was used to evaluate whether participants' hand reports during the clamp block significantly deviated from baseline hand reports. Second, a cluster analysis was used to evaluate whether the hand reports significantly deviated from the actual hand angles during the error clamp and aftereffect blocks.

For Experiment 2, we applied the same cluster permutation analysis to evaluate whether the hand angle data for each cycle deviated from baseline (cycles 6 – 25). However, the cluster analysis was not possible for the hand report data because, unlike Experiment 1, these were only obtained intermittently in Experiment 2, violating the cluster test assumption of continuity (Maris and Oostenveld 2007). Thus, we opted to use a non-parametric permutation t-test to compare hand reports as a conservative means of comparison between error clamp cycles versus baseline reports. We employed a less stringent false discovery rate (FDR = 0.05) procedure (Curran-Everett 2000) to correct for eight planned comparisons, each asking whether the mean hand report value in a given mini-block significantly deviated from the mean of the veridical feedback baseline report mini-blocks. The 8 mini-blocks consist of cycles 26 – 30, 46 – 50, 66 – 70, 71 – 75, 91 – 95, 111 – 115, 131 – 135, and 136 – 140. The selection of these eight planned comparisons was guided by the observations in Experiment 1, asking how subtle feedback sources influence hand reports during distinct phases of learning.

Values are reported as means with 95% confidence intervals within square brackets. For all within-subject comparisons, Cohen's d_z provides a measure of effect size. For each significant cluster identified through the cluster-based permutation t test in Experiment 1, an average Cohen's d_z was provided as a gross measure of effect size. This was calculated using the t-values obtained from each cycle within the given cluster.

Other measures of hand angle

For measures of hand angle in Experiment 1, we report performance at asymptote ("late adaptation"), quantified as the average of the baseline-corrected hand angle data over the last five error clamp cycles (cycles 71 – 75). The inclusion of a no-feedback block in Experiment 1 also allowed us to measure an aftereffect, defined as the baseline-corrected hand angle of the first cycle from this block (cycle 76).

Similar hand angle measures are reported in Experiment 2. Late adaptation was the average of the baseline-corrected hand angle data over the last five cycles of the first error clamp block (cycles 66 – 70) and the last five cycles of the reverse error clamp block (cycles 131 – 135). We also obtained a range measure by taking the difference between these two measures of late adaptation (cycles 131 – 135 minus cycles 66 – 70).

Results

Experiment 1

As expected, participants adapted to the error clamp feedback with the hand angle shifting in the opposite direction of the 15° feedback cursor (Figure 1.2). Based on the permutation test, the hand angle deviated from that observed during the baseline block across a large cluster starting from the third cycle of the clamp block (cycles 26 – 75: $t_{score} = 461.41,\ p_{perm} < 0.001, d_z = 2.3$). The mean deviation in hand angle was 17.6° [7.3°, 27.6°] over the last five cycles of the error clamp block where behavior appeared to be approaching an asymptote.

There was a 5.7° [2.0°, 9.5°] decline in hand angle from late adaptation to the aftereffect block where no feedback was presented. Nonetheless, the deviation in hand angle continued to remain substantially higher than baseline (clamp block cycles 76 - 85: $t_{score} = 81.49,\ p_{perm} < 0.001, d_z = 2.3$), providing a second measure of the degree of implicit adaptation. The mean hand angle in this block started close to that observed at the end of the clamp block (cycle 76: 15.3° [7.7°, 23.8°]) and showed a gradual decline of 3.4° [-2.2, 9.1] over the 10 no-feedback cycles (cycle 85: 12.0° [0.7°, 21.8°]). In summary, we observed robust motor adaptation in response to clamped feedback. Indeed, the response to the clamped feedback was similar to that observed in previous clamp studies (Kim et al. 2018; R. Morehead et al. 2017), indicating that the hand reports had little, if any impact on adaptation.

Subjective reports obtained at the end of experiments using a visual clamp indicate that participants are unaware of their adaptation to the visual clamp (R. Morehead et al. 2017). The main goal of this study was to directly probe participants' awareness of the evolving change in hand angle, asking them to report their hand position after each reach. As can be seen in Figure 1.2, the hand report data dramatically diverged from the actual hand position, confirming that the observed changes in behavior are largely implicit. To quantify the relationship between the change in hand angle and the participants' awareness of these changes, we expressed the change in the reported position of the hand as a function of the change in the actual position of the hand. Thus, a large percentage would indicate a close correspondence between the two measures. Focusing on the last five cycles in the clamp block, hand reports account for only 8.3 % [-2.0 %, 26 %] of hand angle, revealing little correspondence between the two measures. These data are consistent with the post-report survey data in previous studies, indicating that participants are largely unaware of the large change in motor behavior induced by the error clamp.

However, there are systematic changes in the hand report data during the clamp block. Initially, participants report the hand position to be shifted in the direction of the error clamp, that is, in the opposite direction of the behavioral change (clamp block cycles 26 - 29: $t_{score} = 12.78,\ p_{perm} = 0.003$, - 2.17° [-5.8°, 1.2°], $d_z = 1.1$). Interestingly, this effect was strongest right at the onset of the clamp. One possibility is that some participants were confused by the visual clamp and inferred the position of the hand to be the position of the cursor. This hypothesis would predict that a subset of participants would report hand positions near the clamp location (15°). However, only 9% of all trials in the first block across all participants (22 out of 256 reports) had reports greater than 5° (a conservative cut-off), almost half of which was driven by one participant (9 out of 22 reports). Thus, the shift of perceived hand location towards the clamp suggests that the onset of the visual clamp automatically and implicitly biased the hand reports.

Over time, this initial bias gives way to reports that move in the same direction as the change in hand angle. The reported hand position was reliably different than 0° in the same direction as the actual hand position for only a few clusters (clamp block cycles 53 – 55, 61 – 63, 72 – 75: all $t_{score} > 9.07,$ all $p_{perm} < 0.03$, all $d_z > 1.1$). Even here, the mean values were relatively small (1.5° [0.3°, 4.0°]).

There was little to no change in hand reports between the end of the adaptation phase and the start of the aftereffect phase (difference between the average hand reports of cycle 76 and the average hand angle of cycles 72 – 75: 0.1° [-3.6°, 2.8°]), with the hand reports remaining significantly different than baseline in the direction of adaptation (cycles 76 – 83: $t_{score} = 44.7,\ p_{perm} < 0.001, d_z = 1.4$). When veridical feedback was reintroduced for the washout cycles, hand reports increased dramatically to match actual hand angle (cycles 85 – 90: $t_{score} = 43.37,\ p_{perm} < 0.001, d_z = 1.1$). This indicates that the participants understood the task instructions, providing reports of their sensed hand position.

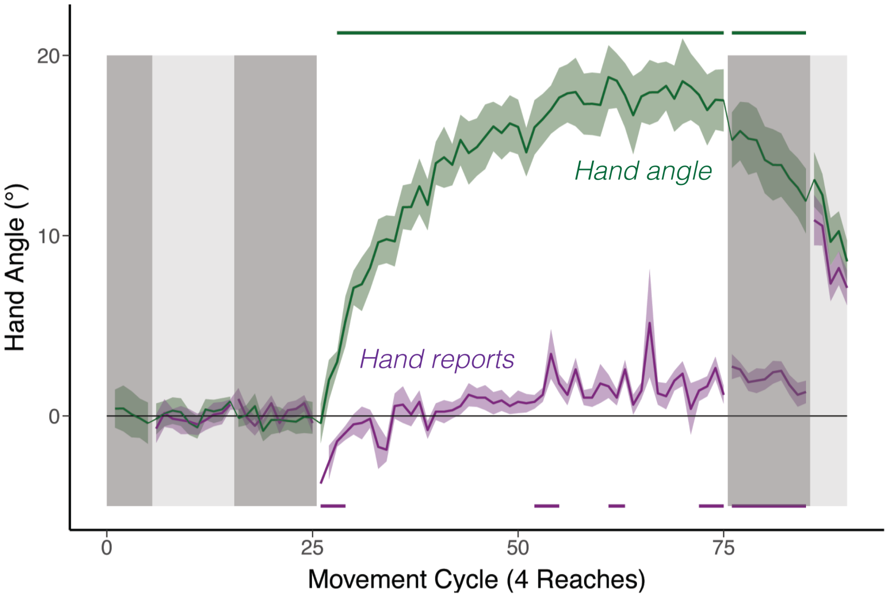

Figure 1.2. Reaching and hand position report functions for Experiment 1. Target position is always at 0°. Vertical shading indicates feedback for each block (light gray: veridical; dark grey: no feedback; white: visual error clamp). Clusters in which hand report (bottom, purple) and hand angle (top, green) data are significantly different than baseline are denoted by the bars at the bottom and top of the graph, respectively. SEM denoted by shaded region around each function.

Experiment 2

Experiment 2 provided a second assay of participants' explicit experience when adapting to a visual clamp. We introduced a few modifications to the task to focus on two questions. First, we had not anticipated the initial shift in the hand report data in the direction of the clamp. We outlined two hypotheses above: 1) Some participants might have initially interpreted the clamp as veridical feedback or 2) participants may be automatically biased to report their hand position in the direction of the visual clamp. While the hand report data in Experiment 1 support the latter view, we added extra instructions and increased the clamp size from 15° to 45°. Increasing the size of the clamp should reinforce the non-veridical nature of the feedback and thus minimize any possible confusion of the clamp with the hand.

Second, we sought to increase the dynamic range of the change in hand angle, providing a larger window over which to observe changes in the hand reports. We expected the asymptotic change in hand angle (from adaptation) would be largely unchanged in response to the larger clamp angle (Kim et al. 2018). Thus, to increase the dynamic range we employed a design in which the direction of the error clamp was reversed at the midpoint of the experiment. This should result in a shift in the direction of the heading angle for the hand, eventually reaching a similar asymptotic value in the opposite direction. We can then examine if the hand report data shows a similar reversal.

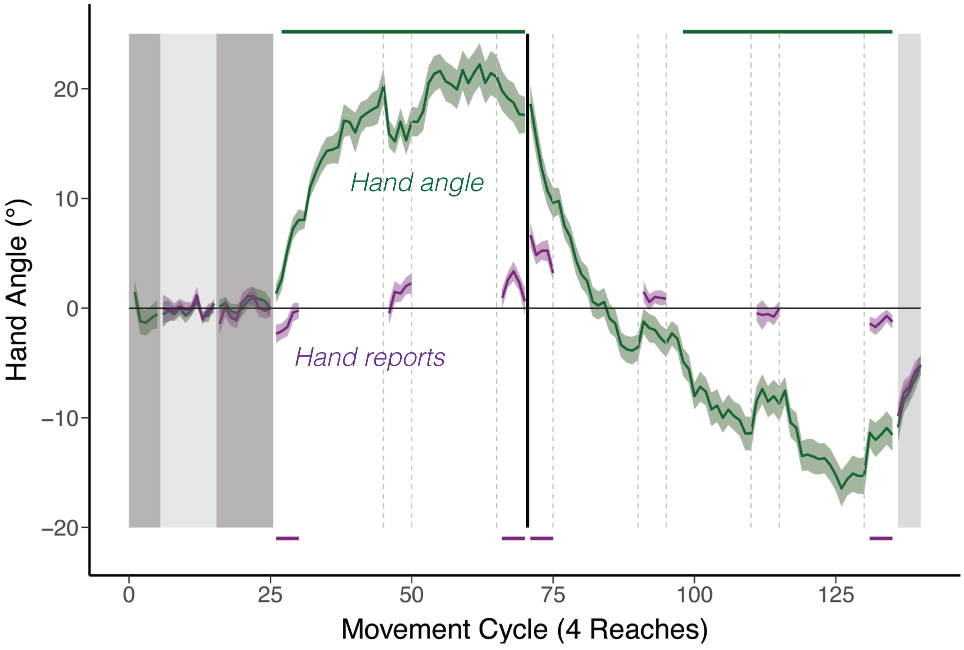

Figure 1.3. Reaching and hand position report functions for Experiment 2. Note that hand reports were only obtained in an intermittent manner. Target position is always at 0°. Vertical shading indicates feedback for each block (light gray: veridical; dark grey: no feedback; white: visual error clamp). Black vertical line denotes cycle 71 where the direction of clamped feedback reverses from 45° to - 45°. Clusters in which hand angle deviated from baseline based on permutation test are indicated by green bars at the top of graph. Mini-blocks of hand report data in which a t-test indicated a difference between hand report data and baseline are indicated by purple bars at bottom of the graph. SEM denoted by the shaded region around each function.

During the initial clamp block, hand angle again deviated in a direction opposite the clamp, the signature of adaptation (Figure 1.3). The shift in hand was significantly different from baseline by the second error clamp cycle (clamp block cycles 27 – 70: $t_{score} = 341.49,\ p_{perm} < 0.001, d_z = 1.9$). Participants reached an asymptotic value of 18.6° [3.5°, 30.6°], similar to the values reported in Experiment 1. When the direction of the clamp was reversed, a corresponding change in hand angle was observed. The mean hand angle crossed the target direction at cycle 85 and reached a maximum (non-asymptotic) mean value of -11.5° [-25.0°, -2.5°]. The deviation in the opposite direction of the clamp was significantly different than the baseline-corrected direction starting at cycle 98 (reversed clamp block cycles 98 – 135: $t_{score} = 203.54,\ p_{perm} < 0.001, d_z = 1.4$). When the effects of the initial and reversed clamp are combined, the summed magnitude of the change in hand angle averaged 30.0° [4.5°, 53.8°].

We sampled the hand report data in an intermittent fashion in Experiment 2 (purple function in Figure 1.3). Focusing initially on the subjective reports at the end of each clamp block, we again observed a marked dissociation between the reported and actual position of the hand, confirming that the observed changes in behavior operated largely in an implicit manner. In the last cycles of the first clamp block, the reported change in hand position was only 8.4 % [-30 %, 40%] (1.9° [-2.3°, 6.2°]) of the actual change in hand position. A similar dissociation was observed in the reversed clamp block where the hand report positions were 16.3% [-17 %, 61 %] (3.2° [-3.5°, 8.9°]) of the actual change in hand angle (with the higher values here due to the fact that adaptation had not reached asymptote in this block).

There were subtle changes in perceived hand position, with a pattern similar to that observed in Experiment 1. Participants again initially perceived their hand position to be shifted in the direction of the clamp, a direction opposite to the evolving change in actual hand position. Given that the hand reports were obtained intermittently, non-parametric permutation paired t-tests were performed, comparing each mini-block of hand report data to baseline. The shift in the direction of the clamp was significant when averaged over the first mini-block (clamp block cycles 26 – 30: $t_{perm} = -3,\ p_{FDR} = 0.01$, -1.4° [-4.2°, 1.5°], $d_z = 0.75$). The mean perceived position of the hand then shifted in the direction of the actual hand position as in Experiment 1, but these shifts were not significantly different from baseline (cycles 46 – 50: $t_{perm} = 1,\ p_{FDR} = 1$, 1.3° [-1.3°, 4.5°], $d_z = 0.25$; cycles 66 – 70: $t_{perm} = 2,\ p_{FDR} = 0.08,\ 2°$ [-2.3°, 6.2°], $d_z = 0.5$).

When the clamp reversed, we again observed a shift in perceived hand position in the direction of the clamp (cycles 71 – 75: $t_{perm} = 4,\ p_{FDR} < 0.001,\ 3.1° \ [-1.9°, 8.4°], d_z = 1$), that then reversed, following the direction of the actual hand position, becoming reliably different than baseline again in the final hand report mini-block (cycles 131–135: $t_{perm} = -3,\ p_{FDR} = 0.02$, $-1.3° \ [-3.3°, 0.9°], d_z = -0.75$). Importantly, even when reliable, the mean of the hand reports remained near the target at a strikingly small value relative to hand position. When veridical feedback was reintroduced during the washout cycles, the hand reports immediately changed, aligning with the actual hand angle (washout cycles 136 – 140: $t_{perm} = -5,\ p_{FDR} < 0.001, d_z = -1.2$). This alignment provides further confirmation that the participants were following the instructions to report their sensed hand position.

Correlation between actual and sensed hand position

In both experiments, the hand reports displayed an initial rapid shift towards the visual error clamp, and a gradual shift in the direction of adaptation that reached a peak of around 2°. We assume the reversal in sensed hand position arises from proprioceptive feedback: As adaptation proceeds, veridical feedback from proprioception would signal a hand position that is shifted in the opposite direction of the visual feedback. Consistent with this hypothesis, we observed a positive correlation between the magnitude of adaptation (change in hand angle) and reported hand position at the end of the clamp block (Figure 1.4: $R_{spearman} = 0.5, p < 0.001$).

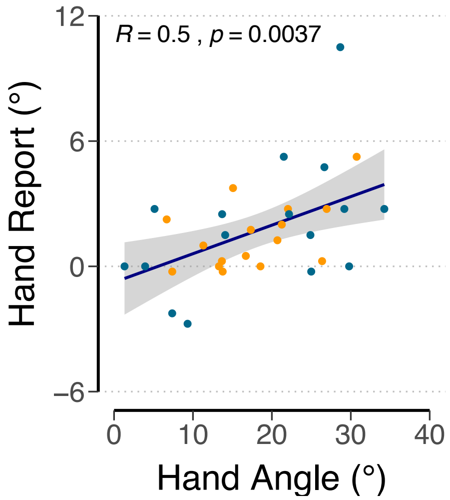

Figure 1.4. Pearson correlation between hand angle and hand reports during late adaptation, pooling together data from Experiment 1 (cycles 71 – 75, yellow dots) and Experiment 2 (end of first clamp block: cycles 66 – 70, blue dots). Correlations are marginally significant if data from each experiment were analyzed separately (Experiment 1: $R_{spearman} = 0.48, p = 0.06$; Experiment 2: $R_{spearman} = 0.42, p = 0.1$), likely reflecting a lack of statistical power. Solid line corresponds to the best-fitting regression line, while the grey shaded region corresponds to the 95% confidence interval.

Discussion

Sensorimotor adaptation is considered an automatic learning process, ensuring that the sensorimotor systems remains calibrated in response to ongoing changes in the state of the body and environmental context (Shadmehr, Smith, and Krakauer 2010). Several lines of evidence highlight the implicit nature of adaptation. Retrospective queries assessing participant's phenomenological experience *after* learning suggest that the change in behavior is largely implicit (at least for rotations up to 30-45°). Perhaps most compelling, participants show persistent aftereffects when asked to reach directly to the target during no-feedback blocks, unable to volitionally modify their behavior after being informed that a perturbation is no longer present. Similarly, even when employing a re-aiming strategy to compensate for a large perturbation, a significant portion of the change in heading angle is unaccounted when the participants are asked to report their intended movement direction prior to the reach (Taylor, Krakauer, and Ivry 2014). Here, taking a more direct approach by probing sensed hand position throughout motor adaptation, we observed a marked dissociation between the participants' behavior and their awareness of that behavior: Overall, the clamped feedback elicited a shift in heading angle of ~18°, yet the phenomenal reports of perceived hand position remained close to the target location, deviating by only ~2°. Thus, the current results confirm that participants are largely unaware of the behavioral consequences of automatic adaptation.

Methodological Considerations

These observations provide strong support that the behavioral change in adaptation studies occurs in an automatic and implicit manner. However, it has been unclear from past methods whether participants are aware of the behavioral changes themselves. Probes of awareness obtained at the end of the experiment yield limited information and may be problematic. First, these retrospective queries are generally framed in a binary manner such as "Did you reach to the target throughout the whole experiment" or "Were you aware of any changes in your hand position", whereas the underlying reality may resemble more of a continuum, with one's awareness of hand position varying throughout the course of adaptation. Second, questionnaires, especially those administered the end of the session, make it difficult for participants to confidently recall their phenomenal experience (Werner et al. 2015). Moreover, in a standard adaptation study, the task error becomes quite small at the end of the adaptation block. This reduction in perceived error may impact subsequent recall (i.e., a recency effect).

To more directly assess the participants' phenomenal experience over the course of adaptation, we asked the participants to maintain their hand position at the end of the movement and report the angular position of the hand with respect to the target. While this report procedure could be used with standard, contingent visual perturbations, we opted to use the clamp method because it offers two, distinct advantages. First, the behavioral change in response to the clamp is assumed to arise solely from implicit processes given that participants are actively discouraged from using an aiming strategy. Second, the perceived "error" remains invariant since the angular direction of the feedback is fixed; with standard methods, the size of the error is in constant flux and this variability might influence the hand report data.

Conversely, a report procedure such as that employed here would be problematic with standard methods of adaptation in which the feedback is contingent on actual hand position. Consider first procedures in which the perturbation is introduced as an abrupt step-change (e.g., onset of 45° rotation). Here, some degree of learning will likely include the use of strategic aiming, with the degree and form of the strategy changes across trials highly idiosyncratic across individuals (Taylor, Krakauer, and Ivry 2014). The aiming changes would surely influence the reports of hand position, similar to the way the reports in the clamp method appear to be dominated by the instruction to aim to the target (see below). Methodologically, it would be difficult to estimate how the reports are influenced by strategic processes and sources of feedback.

Alternatively, one could use contingent feedback, but introduce the rotation in a gradual manner (e.g., increase by 1° every few trials). As long as the upper bound on the perturbation is kept 25-30°, it is likely that many participants would remain aware of the imposed perturbation (if asked in a post-session survey). As such, strategic processes should be eliminated and allow for a comparison with the results from the current experiments. In such an experiment, we expect that the sensed hand position would be modulated by the same processes as with our clamped feedback. However, the gradual method has one serious limitation. Assuming that participants remain unaware of the perturbation, they will treat the cursor as veridical and thus, when queried about their felt hand position, are likely to simply report the cursor.

Mechanisms Underlying Sensed Hand Position

The hand report data were not randomly centered about the target as would be expected if participants were completely oblivious of the consequences of adaptation. Rather, two systematic changes in the hand reports were observed in both experiments. First, the perceived location of the hand was biased towards the clamped feedback right at the onset of the error clamp block. This effect was similar in response to the introduction of either a 15° or 45° clamp. As such, it seems unlikely to reflect trials in which participants confused the clamped feedback as their veridical hand position. Instead, this initial bias is reminiscent of the proprioceptive shift reported in studies of visuomotor adaptation where the perceived estimate of hand position gravitates towards the visual perturbation (Henriques and Cressman 2012; Ruttle et al. 2016). These proprioceptive shifts have been interpreted from an optimal integration perspective, whereby sensory discrepancies between vision and proprioception generate a unified estimate of hand position (Ernst and Banks 2002). This initial bias, observed in both experiments, is consistent in magnitude (3° - 4° towards the visual feedback) and rapid onset with the proprioceptive shift reported in previous studies (Ruttle et al. 2016; Salomonczyk, Cressman, and Henriques 2011; Cressman and Henriques 2009, 2010). Interestingly, the biasing effect of the feedback appears to be even stronger when reaches are made in the absence of a visible target (Synofzik et al. 2010).

Second, this bias gave way to a reliable shift in the reported hand position in the direction of adaptation (i.e., away from the visual feedback) that reached a peak of around ~2°. The reversal in the perceived location of the hand may arise from proprioceptive feedback: As adaptation proceeds, veridical proprioceptive feedback would signal a hand position that is shifted in the opposite direction of the visual feedback. Consistent with this hypothesis, we observed a positive correlation between the magnitude of adaptation (change in hand angle) and reported hand position at the end of the clamp block. Despite this correlation, it is important to keep in mind that there remains a large discrepancy between the actual and reported hand position, with the latter remaining close to the target. The lack of sensitivity to the substantial changes in hand angle induced by the clamp may, in part reflect the relatively poor acuity of proprioception, at least when probed in a static manner (Jones, Cressman, and Henriques 2010).

The subtle changes in perceived hand position suggest that these data encompass two, distinct contributions from proprioception, one associated with biases induced from the visual feedback (i.e., the proprioceptive shift), and the other associated with veridical hand position. Nonetheless, the most striking feature of the data is that the hand reports remain close to the target location. This illusory experience likely reflects strong constraints arising from the task goal, namely, to reach to a visual target. We propose that this goal elicits additional sources of information that have a major impact on perceived hand position in the face of adaptation. One source could be the visual target itself: Similar to how the feedback cursor introduces a bias into judgments of hand position, the target may also serve as a salient source of bias given that the participants were, presumably, aiming to this location. The feedforward signal associated with a motor plan to reach to the target could also be a source of information (Izawa and Shadmehr 2011; Ruttle, Hart, and Henriques 2020). That is, participants have a strong prior to anticipate the hand will terminate in a position close to where they intend to move. With clamped feedback, this position is at the target.

In conclusion, by obtaining continuous probes of sensed hand position, our results confirm that participants are largely unaware of the behavioral changes that occur during implicit sensorimotor adaptation, but also reveal the subtle influences of sensory feedback on their subjective experience. To return to our opening example, the tired ping-pong player may be well aware of her state but is largely insensitive to the changes enacted by her brain to compensate for her fatigue.

Chapter 2: Individual differences in proprioception predict the extent of implicit sensorimotor adaptation

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In this Chapter, I evaluate whether there is a relationship between kinesthetic perception and the upper bound of implicit adaptation: Recent studies have revealed an upper bound in motor adaptation, beyond which other learning systems may be recruited. The factors determining this upper bound are poorly understood. The multisensory integration hypothesis states that this limit arises from opposing responses to visual and proprioceptive feedback. As individuals adapt to a visual perturbation, they experience an increasing proprioceptive error in the opposite direction, and the upper bound is the point where these two error signals reach an equilibrium. Assuming that visual and proprioceptive feedback are weighted according to their variability, there should be a correlation between proprioceptive variability and the limits of adaptation. Alternatively, the proprioceptive realignment hypothesis states that the upper bound arises when the (visually biased) sensed hand position realigns with the expected sensed position (target). When a visuo-proprioceptive discrepancy is introduced, the sensed hand position is biased towards the visual cursor, and the adaptive system counteracts this discrepancy by driving the hand away from the target. This hypothesis predicts a correlation between the size of the proprioceptive shift and the upper bound of adaptation. We tested these two hypotheses by considering natural variation in proprioception and motor adaptation across individuals. We observed a modest, yet reliable correlation between the upper bound of adaptation with *both* proprioceptive measures (variability and shift). While the results do not clearly favor one hypothesis over the other, they underscore the critical role of proprioception in sensorimotor adaptation.

Introduction

Accurate motor control requires the continuous calibration of the sensorimotor system, a process driven by the sensory feedback experienced over the course of movement. One of the primary learning processes involved in keeping the system calibrated is implicit sensorimotor adaptation (Tseng et al. 2007; Shadmehr, Smith, and Krakauer 2010; Taylor, Krakauer, and Ivry 2014). Here, learning is assumed to be driven by sensory prediction error (SPE), the difference between the predicted feedback from a motor command and the actual sensory feedback.

Recent findings have shown that implicit adaptation in response to a visuomotor rotation (VMR) is remarkably invariant across a large range of error sizes and tasks (R. Morehead et al. 2017; Kim et al. 2018). Even in response to large errors (e.g., 45°), the maximum amount of trial-to-trial change is around 1° - 2° (R. Morehead et al. 2017; Kim et al. 2018; Bond and Taylor 2015; Wei and Körding 2009; Vandevoorde and Orban de Xivry 2019; Herzfeld et al. 2014) – not surprising for a system that likely evolved to adjust for subtle changes in the environment and body. More puzzling, the maximum degree of plasticity within this slow learning system is limited, maintaining an asymptotic value of around 15° - 25° even after hundreds of trials (Kim et al. 2018; Bond and Taylor 2015; R. Morehead et al. 2017; Dang, Parvin, and Ivry 2019; Werner et al. 2015; M. K. Rand and Heuer 2019; A. M. Haith, Huberdeau, and Krakauer 2015) or across multiple test sessions (Wilterson and Taylor 2019; Stark-Inbar et al. 2017). As such, learning to compensate for large errors requires the recruitment of other learning processes such as explicit aiming strategies (A. M.

Haith, Huberdeau, and Krakauer 2015; McDougle and Taylor 2019; Huberdeau, Haith, and Krakauer 2015; Hegele and Heuer 2010).

Although the mean upper bound for implicit adaptation to large visuomotor rotations averages around 20º, individual differences can be quite substantial. In standard VMR tasks, these differences are hard to detect during learning since participants eventually exhibit near-perfect performance, independent of the size of the perturbation. With these tasks, the individual differences become evident during the "washout" phase when feedback is eliminated, and participants are instructed to reach directly to the target. An alternative method is to use non-contingent, "clamped" visual feedback in which the angular trajectory of the feedback cursor is invariant, always following a path that is deviated from the target by a fixed angle (e.g., 15º). Despite instructions to ignore this feedback, the participants' behavior reveals an automatic and implicit adaptation response, deviating across trials in the opposite direction of the clamp (Jonathan Sanching Tsay, Parvin, and Ivry 2020; R. Morehead et al. 2017; Kim et al. 2018). With this method, the error remains constant across trials; as such, the asymptote is not tied to changes in task performance (i.e., feedback terminating closer to the target), but rather, the asymptote reflects endogenous constraints. Across both methods (washout performance in tasks using contingent feedback or asymptotic performance in response to non-contingent feedback), the range of values is considerable. For example, in one study (Kim et al. 2018), the range of asymptotes in response to 15º clamped feedback was between 12º and 43º (mean = 18º, sd = 10º).

The factors which determine the upper bound of implicit adaptation are poorly understood. One hypothesis is that the limit reflects the interaction of visual and proprioceptive feedback. As adaptation progresses, the hand movements are adjusted away from the target, reducing the visual SPE (at least in standard VMR tasks). However, the change in hand direction away from the target results in an increase in a proprioceptive SPE, the difference between the expected and experienced signals of hand position. Importantly, the direction of the proprioceptive SPE is opposite to that of the visual SPE, and thus the response to these two SPEs are in the opposite directions. The asymptotic level of adaptation may thus reflect an equilibrium between learning from visual and proprioceptive error signals.

Studies of multisensory integration have shown that when participants estimate the location of their hand, they use a combination of visual and proprioceptive feedback, weighting each source based on their relative *reliability* (Robert J. van Beers 2012; R. J. van Beers, Sittig, and Denier van der Gon 1998; Robert J. van Beers, Wolpert, and Haggard 2002; Burge, Ernst, and Banks 2008; Ernst and Banks 2002; Sober and Sabes 2003). Consistent with this hypothesis, in the context of visuomotor adaptation, the response to a visual perturbation is reduced when noise is added to the visual feedback (Burge, Ernst, and Banks 2008; Wei and Körding 2010; Jonathan S. Tsay, Avraham, et al. 2021; Körding and Wolpert 2004; Robert J. van Beers 2012). The corollary prediction, namely that the response to a visual perturbation should increase as a function of noise (i.e., variability) within the proprioceptive system, has not been tested.

A second hypothesis relates to another way in which visual and proprioceptive information have been shown to interact during adaptation. The introduction of a visual perturbation creates a discrepancy between the visual and proprioceptive feedback. This discrepancy results in a shift in the perceived location of the hand towards the visual feedback, a phenomenon referred to as a "proprioceptive shift." The size of the shift tends to range between 5º - 10º, and remains relatively stable, evidenced by probing sensed hand position following passive hand displacement at various timepoints in an adaptation study (Ruttle, 't Hart, and Henriques 2018; Cressman and Henriques 2009, 2010; Gastrock, Modchalingam, Hart, et al. 2020; Modchalingam et al. 2019; Vachon et al. 2020; Rossi, Bastian, and Therrien 2021; H. J. Block and Bastian 2011; M. K. Rand and Heuer

2019). Similar to multisensory integration, this shift presumably reflects the operation of a system seeking to establish a unified percept from discrepant sensory signals.

The processes underlying proprioceptive shift may also contribute to the upper bound of implicit adaptation. This shift introduces a different error signal, the discrepancy between the target and the sensed hand position (i.e., the difference between the expected trajectory to the target and the trajectory towards the perceived hand position). A learning process seeking to counteract this error signal would also drive the hand direction away from the perturbation (i.e., the opposite direction of the proprioceptive shift). By this view, implicit adaptation would reach an asymptote when the sensed hand position is "realigned" with the target, and as such, the asymptote would correlate with the size of the proprioceptive shift: A larger deviation in hand angle would be required to counteract a large proprioceptive shift.

To examine these two hypotheses in tandem, we exploit natural variation across individuals, examining the relationship between individual differences in proprioceptive variability and proprioceptive shift with the upper bound of implicit adaptation. To measure proprioception, participants were asked to report the position of their hand after passive displacement. These proprioceptive probes were obtained before, during, and after an extended block of trials in which the visual feedback was perturbed. From these data, we could use standard psychophysical methods to estimate for each participant, the bias and variability in their sense of proprioception, with the bias providing an assay of proprioceptive shift. In Experiment 1, the upper bound on implicit adaptation was estimated by measuring the participants' aftereffect in response to a response-contingent visuomotor rotation. In Experiment 2, the upper bound was estimated using the asymptotic response to clamped visual feedback.

A.

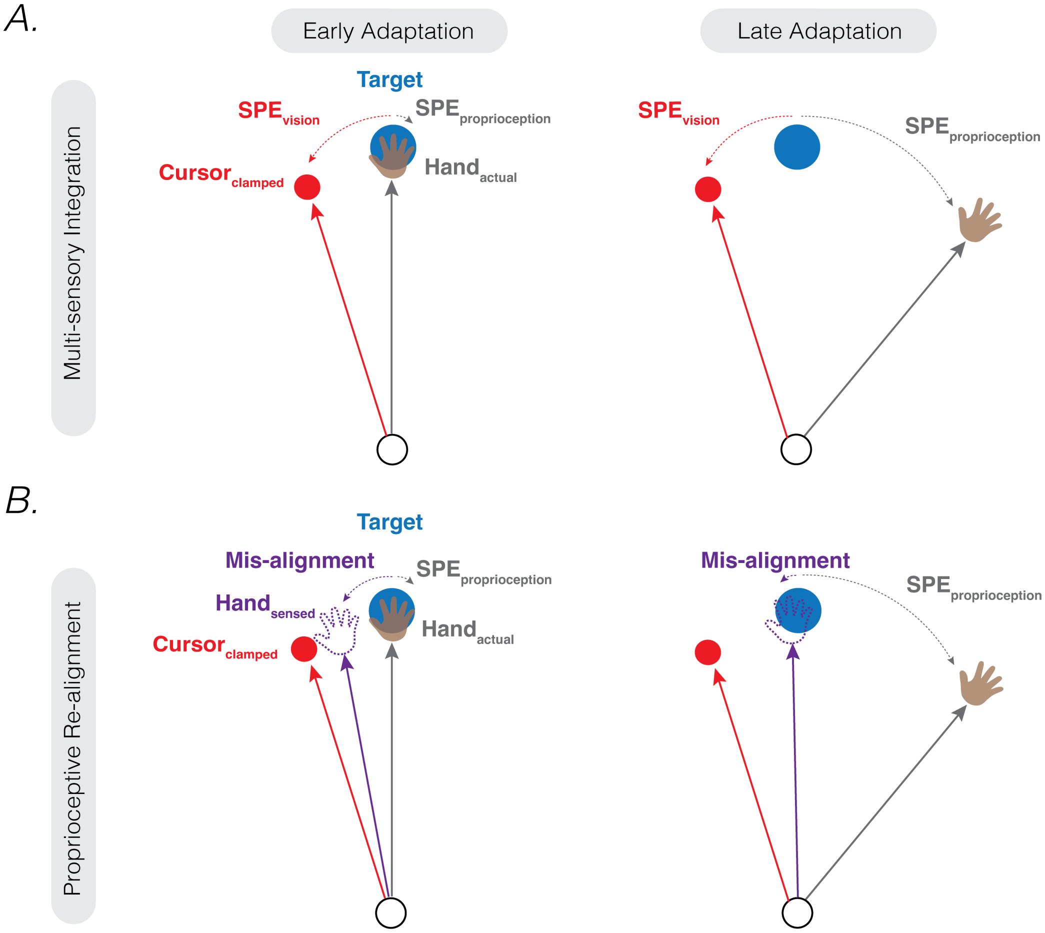

Figure 2.1. Two hypotheses concerning constraints on the upper bound of implicit adaptation. **A)** By the multisensory integration hypothesis, the upper bound of adaptation is the point of equilibrium between the visual SPE and the proprioceptive SPE. Since there is typically more variability in proprioception compared to vision, the proprioceptive SPE may be weighted less, requiring a greater proprioceptive SPE to offset a visual SPE. **B)** By the proprioceptive realignment hypothesis, the upper bound of adaptation occurs when the participant's sensed hand position is at the target. Sensed hand position is a composite of visual-based inputs underlying the proprioceptive shift (target and cursor) and proprioception from the true hand position.

Methods

Participants

Undergraduate students were recruited from the UC Berkeley community (Exp 1 N = 30; Exp 2 N = 32; age = 18 – 22; 45 women, 17 men) and either received course credit or financial compensation for their participation. As assessed by the Edinburgh handedness inventory, all of the participants were right handed (Oldfield 1971). The protocol was approved by the IRB at UC Berkeley.

Experimental overview

Each experiment involved a mix of reaching trials and proprioceptive probe trials. For both tasks, the participants were seated in front of a custom tabletop setup and placed their hand on a digitizing graphics tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA, sampling rate = 200

Hz.) that was horizontally aligned with and positioned below an LCD monitor (53.2 cm by 30 cm, ASUS). The participant's view of their hand was occluded by the monitor, and the room lights were extinguished to minimize peripheral vision of the arm. On reaching trials, arm movements were made by sliding a digitizing pen, embedded in a custom handle, across the table. On proprioceptive trials, the participant held the digitizing pen, and the experimenter moved the participant's arm.

Reaching Trials

Reaches were made from a start location to a target, located at various locations (see below). The start location was indicated by a white ring (6 mm diameter) and the target by a blue circle (6 mm diameter), with the radial distance between the start location and target fixed at 16 cm. To initiate a trial, the participant moved her hand to the start location. Visual feedback of the hand position was given via a cursor (white circle 3.5 mm diameter) only when the hand was within 1 cm of the start position. Once the hand remained within the start location for 500 ms, the target appeared, serving as a cue to indicate the location of the target and an imperative to initiate the reach. To discourage on-line corrections, participants were instructed to perform 'shooting' movements, making a rapid movement that intersected the target.

There were two types of feedback trials: veridical and perturbed. On veridical trials, the cursor corresponded to the position of the hand. On perturbation trials, the cursor was either rotated relative to the hand position (visuomotor rotation, Exp 1) or restricted to an invariant path along a constant angle with respect to the target (visual clamp, Exp 2). On feedback trials, the radial position of the cursor matched the radial position of the hand until the movement amplitude reached 16 cm (the radial distance of the target), at which point the cursor froze. On no-feedback trials, the cursor was blanked when the target appeared, and did not re-appear until the participant had completed the reach and returned to the start location for the next trial.

Movement time was defined as the interval between when the hand movement exceeded 1 cm from the start position to when the radial distance of the movement reached 16 cm. To ensure that the movements were made quickly, the computer played a prerecorded message "too slow" if movement time exceeded 300 ms. If the movement time was less than 300 ms, a neutral 'knock' sound was generated, informing the participant that the reach speed had fallen in the acceptable window. There were no constraints on reaction time.

Proprioceptive Probe Trials

To probe proprioceptive variability, the experimenter sat at the opposite side of the table, across from the participant. From this position, the experimenter could passively move the participant's right hand to different probe locations (see below). The participant was instructed to hold the digitizing pen, but to maintain a passive state, one that allowed the experimenter to move the participant's right hand with minimal resistance. To produce the passive movements, the experimenter used her left hand to move the participant's right hand, maintaining contact throughout the proprioceptive probe block.

The experimenter initiated each trial by moving the participant's hand into the start position, at which point the word 'Ready' appeared on the screen. The experimenter then hit the space bar with her right hand, at which point the word 'Ready' disappeared and a number specifying the desired target location appeared on the corner of the monitor closest to the experimenter (Figure 2.2). A small cloth cover was placed at this corner to prevent the participant from seeing the number. The experimenter moved the participant's hand to the specified target location. Once the participant's hand was at the target location (2 cm diameter tolerance window), the word 'Ready' again appeared and the experimenter hit the space bar to advance the trial. A filled white circle (3.5 mm diameter) then appeared at a random position on the monitor. The participant used her left hand to move a mouse (Logitech Trackman Marble), positioning the cursor above the sensed position of their right hand. When satisfied with the position of the cursor, the participant clicked the mouse button. The participant was allowed to modify their response by repositioning the mouse and clicking again. When the participant confirmed that the trial was complete, the experimenter hit the space bar, at which point the cursor disappeared. The experimenter then moved the participant's hand back to the start position to initiate the next trial. The start position remained on the screen for the duration of the proprioceptive probe trials.

We opted to use a tolerance window of 2 cm in positioning the hand, a value that was large enough for the experimenter to guide the participant's hand to the target location without feedback, but also small enough to ensure minimal variation in target positions across trials. Note that variance in the position of the hand was irrelevant given that the proprioceptive judgments were recorded as the difference from the perceived location of the hand (mouse click) and the actual position of the hand.

Experiment 1, Movement-contingent, rotated feedback

Reaching and proprioceptive trials were performed to 5 targets located within a wedge (at 70º, 80º, 90º, 100º, 110º, with 90º corresponding to straight ahead). The trials were arranged in cycles of one trial per target, with the order randomized within a cycle.

The experiment began with a brief phase to familiarize the participants with the reaching task. This consisted of 10 baseline reaching trials in which no visual feedback was provided, followed by 10 baseline trials with online, veridical feedback. The latter was used to emphasize that the movement should be produced to shoot through the target and demonstrate that the feedback would disappear once the movement amplitude exceeded the radial distance of the target.

The participant then completed a block of 50 baseline proprioceptive probe trials. Following this, the reaching task resumed but now the feedback perturbed. To minimize awareness of the perturbed feedback, the angular deviation of the cursor was increased in small, incremental steps of 0.33º per trial, reaching a maximum of 30º after 90 trials. Across participants, we counterbalanced the direction of the rotation (clockwise or counterclockwise).

Following the initial 90 perturbation trials, the participant then completed 7 more blocks, alternating between proprioceptive probe trials (30 per block) and reaching trials (40 per block, at the full 30º rotation). With this alternating schedule, we sought to obtain stable measures of proprioception following adaptation, while minimizing the effect of temporal decay on adaptation. These blocks were intermixed with four blocks of 5 no-feedback trials with instructions to reach directly to the target despite the absence of feedback. These no-feedback blocks occurred after the first gradual perturbation block, the second fixed perturbation block, the third perturbation block, and the fourth proprioceptive probe block. These no-feedback trials provided the primary data for our measure of adaptation. By having four of these probes, we were also able to assess the time course of adaptation. To complete the session, the participants completed 50 reaching trials with veridical feedback to ensure that the residual effects of adaptation were removed.

Each participant returned for a second session, 2 to 14 days after the first session. The experimental protocol was identical on day 2, allowing us to assess test-retest reliability of the various measures of adaptation and proprioception.

Experiment 2, non-contingent, clamped feedback

The key change in Exp2 was the use of the visual clamp method during the perturbation trials. This form of feedback has been shown to produce robust adaptation with minimal awareness (R. Morehead et al. 2017; Kim et al. 2018; Jonathan Sanching Tsay, Parvin, and Ivry 2020). Moreover, adaptation with this method will reach an upper bound that is not constrained by performance error (e.g., distance between cursor and target which is reduced over time with contingent feedback as in Exp 1), but presumably reflects factors intrinsic to each participant. Based on previous work, we expected to observe a broad range of upper bounds across our sample, a desirable feature to examine individual differences.

The basic method for the reaching and proprioceptive probe trials was similar to that used in Exp 1 with a few changes. First, we used a finer sampling of the workspace for the proprioception task, with target locations spaced every 5º (70º, 75º, 80º, 85º, 90º, 95º, 100º, 105º, 110º). Although participants were not explicitly queried in Exp 1, we were concerned that some participants may have noticed that there were only five discrete target locations, which could potentially bias their responses; that is, the proprioceptive reports might be based on their memory of a previously reported hand position rather than relying solely on the current proprioceptive signal. The finer sampling should reduce the utility of memory-based reports. Second, for the reaching task, we opted to keep the spacing as in Exp 1 (10º apart) but increased the size of the wedge, with the target locations spanning the range of 50º - 130º. This change was motivated by pilot work suggesting that adaptation to a visual clamp is more consistent when the movements are made in a larger workspace. Note that it was necessary to limit reaching in one direction, away from the body, given the workspace limitations imposed by the tablet and our decision to have the movement amplitude be 16 cm.

We also modified the block structure. Experiment 2 began with a proprioception block (one cycle, 1 trial per 9 targets) to familiarize the participant with this task. The participants then completed a block of reaching trials without visual feedback (9 targets, 27 trials total), followed by a block of reaching trials with veridical feedback (72 trials) and another proprioception block (72 trials, with a break after 36 trials).

The participant then completed the perturbation block, composed of 180 trials (break after the first 90). For these trials, the cursor always followed a 16 cm straight trajectory offset by 15º from the target (clockwise or counterclockwise, counterbalanced across participants). The radial distance of the cursor, relative to the start position, was yoked to the participant's hand. Thus, the motion of the cursor was temporally correlated with the participant's hand, but its direction was fixed, independent of the angular position of the participant's hand. Just before the start of this block, the error clamp was described to the participant and she was told to ignore this "feedback" signal, always attempting to reach directly to the target. To help the participant understand the invariant nature of the clamp, three demonstration trials were provided. On all three, the target appeared straight ahead at 90º and the participant was told to reach to the left (demo 1), to the right (demo 2), and backward (demo 3). On all three of these demonstration trials, the cursor moved in a straight line, 15º offset from the target. In this way, the participant could see that the spatial trajectory of the cursor was unrelated to their own reach direction.

Following the initial 90 trials with clamped feedback, the participant completed seven blocks, alternating between the proprioception task (36 trials/block, four blocks) and the reaching task with clamped feedback (90 trials/block, three blocks). Given the high reliability in our hand angle and proprioceptive measures from Exp 1 (Figure 2.4A-C), we limited testing to a single session.

Data Analysis

The experimental software and analyses were performed using custom scripts in MATLAB and R.

The evaluation of our core hypotheses involves three variables of interest: Implicit adaptation, proprioceptive shift, and proprioceptive variability. The dependent variable for implicit adaptation was the change in hand angle from baseline, where hand angle was defined as the signed angular difference between the position of the hand at peak velocity and target, relative to the start location.

In Exp 1, the measure of implicit adaptation was the hand angle during the no-feedback aftereffect trials (blocks 2 and 3 averaged across both days since adaptation was at asymptote by block 2). In Exp 2, we used the mean hand angle during the last three blocks (block 2 - 4) of the error clamp trials since adaptation had reached a stable asymptote by block 2. For both experiments, the adaptation analyses were performed after correcting for any bias observed during the last two baseline cycles (Exp 1: 10 trials; Exp 2: 18 trials). Trials in which the hand angle exceeded three standard deviations from a moving 5-trial average were excluded from the analyses (Exp 1: 1.2% ± 0.6% per participant; Exp 2: 0.5% ± 0.3% per participant).

For proprioception, we recorded the x and y coordinate of each hand location report and calculated the angular deviation from the target. Proprioceptive shift was operationalized as the angular difference between the mean sensed hand position for each proprioceptive report block and the mean sensed hand position on the baseline block. For each block, we also calculated the standard deviation of the proprioceptive reports for each block, our measure of proprioceptive variability.

Exp 1 dependent measures were entered into a linear mixed effect model (R function: lmer), with Block and Day as fixed factors, and Participant ID as a random factor. Exp 2 dependent measures were entered into a linear mixed effect model, with Block as the only fixed factor and Participant ID as the random factor. All post-hoc t-tests were two-tailed, and Bonferroni corrected for multiple comparisons. Standard effect sizes are reported (η_p^2 for fixed factors; Cohen's d_z for within-subjects t-tests) (Lakens 2013). When the data met the assumption of normality as assessed with the Shapiro-Wilk test, the parametric Pearson correlation measure was used (R); when normality was violated, we used the non-parametric Spearman correlation (R_s).

We also performed a multiple regression analysis (R function: lm) on the upper bound of adaptation, comparing a model with proprioceptive shift *and* proprioceptive variability as fixed factors to models in which only one of these was included. Given that the former contains two predictors and the latter two each contain only one predictor, we evaluated these fits with R_{adj}^2 (Miles 2014). R_{adj}^2 would only increase if additional parameters improved the model fit more than would be expected by chance.

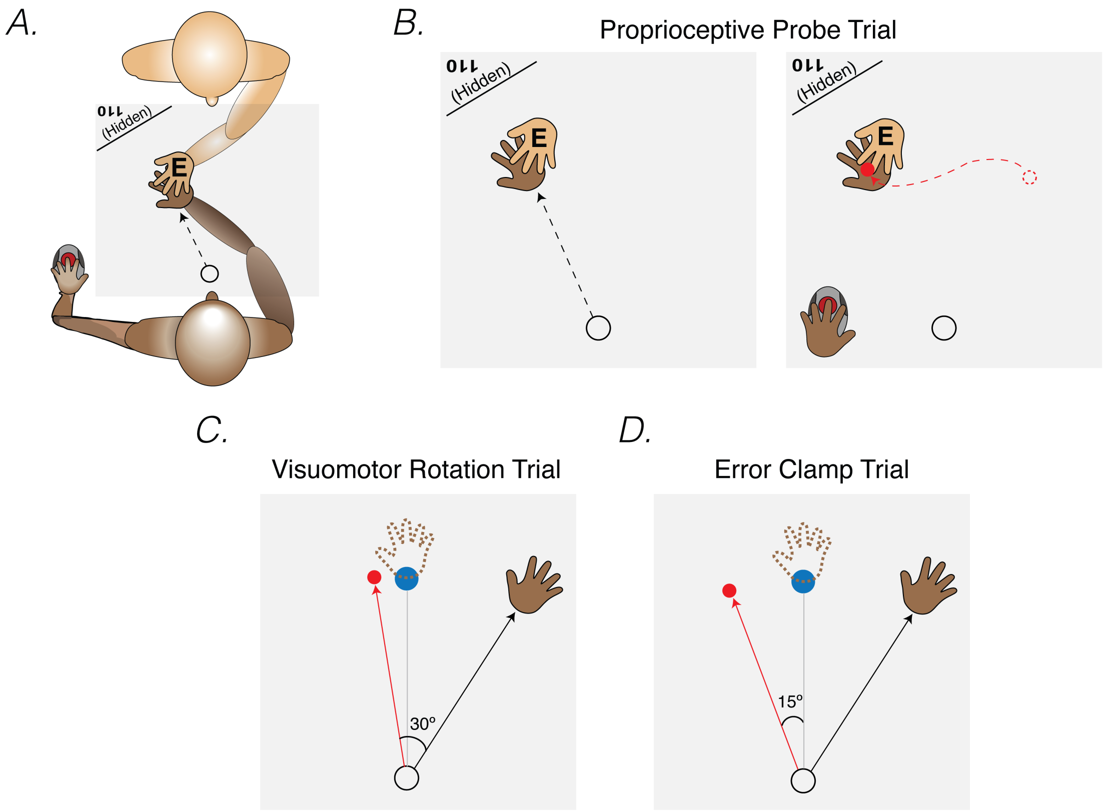

Figure 2.2. Experimental overview. **A)** Experimental setup for proprioceptive probe trials. The experimenter (top, with their hand labeled with an 'E') sat opposite the participant (bottom) and moved their hand from the start position to a specified location. The location (e.g. 110º) was signaled to the experimenter via text which appeared on the corner of the horizontal monitor, behind a cloth which prevented the participant from seeing the text. **B)** After the participant's hand was passively moved to the probe location, a cursor appeared at a random position on the screen. The participant used their left hand to move the cursor to the sensed hand position. **C)** In Exp 1, a rotation was applied to the cursor. The task error introduced by the rotation is nullified if the participant moves in the opposite direction of the rotation. **D)** In Experiment 2, the cursor was clamped, independent of hand position. Participants were told to ignore the error clamp and aim straight for the target. The depicted trials in Panels C and D provide examples of performance late in the adaptation block.

Formalizing the relationship between proprioception and adaptation

In this section, we outline formalizations of the multisensory integration and proprioceptive realignment hypotheses. In the main body of the paper, these formalizations are provided to make explicit the assumptions underlying each hypothesis and, of primary importance, their respective predictions concerning the relationships between measures of proprioception and the upper bound of implicit adaptation. Model-based analyses are presented in the Supplemental Discussion.

Under the multisensory integration hypothesis, adaptation should reach asymptote when the sensory prediction error created by the discrepancy between the cursor and target (μ_{vis}) is offset by the sensory prediction error created by the discrepancy between the hand and target (μ_{prop}). These two error signals are weighted based on uncertainty (σ_{prop}^2 for proprioceptive estimate; σ_{vis}^2 for the visual estimate).

2.1 $$\frac{\sigma_{vis}^2}{\sigma_{vis}^2 + \sigma_{prop}^2} * \mu_{prop} = \frac{\sigma_{prop}^2}{\sigma_{vis}^2 + \sigma_{prop}^2} * \mu_{vis}$$

The hand position that corresponds to the upper bound of adaptation ($\mu_{prop,UB}$) can be calculated based on:

2.2 $$\mu_{prop,UB} = \frac{\sigma_{prop}^2}{\sigma_{vis}^2} * \mu_{vis}$$

Based on (Eq 2.2), the upper bound of adaptation ($\mu_{prop,UB}$) should be positively correlated with proprioceptive variability (σ_{prop}^2).

Under the proprioceptive realignment hypothesis, adaptation will reach asymptote when the sensed hand position is at the target (i.e., 0). The sensed hand position is a combined signal, where actual hand position (μ_{prop}) (weighted by a prior belief that the hand will be at the target) gets calibrated by (i.e., shifts toward) the visual feedback (proprioceptive shift: PS). This shift is driven by cross-sensory calibration of vision *on* proprioception.

While the computational rules governing proprioceptive shifts remain an open question, we assume that the size of this proprioceptive shift is determined solely by the difference between the visual feedback and target position (likely in a non-linear manner) ('t Hart, Ruttle, and Henriques 2020). The literature indicates that this shift occurs quickly (within three trials) (Ruttle et al. 2016; Ruttle, 't Hart, and Henriques 2018; Ruttle, Hart, and Henriques 2020) and remains relatively invariant. Importantly, for present purposes, the size of the shift should be independent of proprioceptive variability (Ayala, Marius 't Hart, and Henriques 2020; H. J. Block and Bastian 2011) (also see: Figures 2.4F and 2.6C).

2.3 $$\frac{\sigma_{prior}^2}{\sigma_{prior}^2 + \sigma_{prop}^2} * \mu_{prop} + PS = Sensed\ Hand\ Position$$

2.4 $$\frac{\sigma_{prior}^2}{\sigma_{prior}^2 + \sigma_{prop}^2} * \mu_{prop,UB} + PS = 0$$

2.5 $$\mu_{prop,UB} = -PS * \frac{\sigma_{prior}^2 + \sigma_{prop}^2}{\sigma_{prior}^2}$$

Based on (Eq 2.5), the upper bound of adaptation ($\mu_{prop,UB}$) should be negatively correlated with proprioceptive shift. In other words, the more proprioception is shifted towards vision, the more adaptation is required to realign sensed hand position with the target. In this model, proprioceptive variability also modulates the upper bound, vis-à-vis its role in determining the optimal hand position in the absence of vision.

Results

Experiment 1

The main goal of Exp 1 was to examine the relationship between individual differences in implicit adaptation and individual differences in proprioception (proprioceptive shift and proprioceptive variability). For implicit adaptation, we focus on the change in heading angle on trials without feedback (aftereffect) following exposure to a 30º rotation of the visual feedback. Since the perturbation was introduced in a gradual manner, we assume the resulting recalibration of the sensorimotor map was implicit.

Implicit Adaptation

In order to track the time course of implicit adaptation, we measured mean hand angle during four no-feedback blocks, one at the end of the baseline block and three during the adaptation phase. There was a main effect of block (Figure 2.3B) ($F_{4,261} = 93.0\ p < 0.001, \eta^2 = 0.85$), with the mean hand angles in each no-feedback block significantly different from baseline ($all\ t_{261} > 24.1,\ p_{bf} < 0.001, d_z > 4.4$). The mean hand angle increased from aftereffect block 1 to aftereffect block 2 (Figure 2.2A, $t_{261} = 5.5,\ p_{bf} < 0.001, d_z = 1.0$). There was no significant difference between the means in the second and third aftereffect blocks ($t_{261} = 0.5,\ p_{bf} = 1$, $d_z = 0.01$), suggesting that implicit adaptation in response to a 30º rotation saturated between 22□ - 26□. The mean hand angle in the fourth aftereffect block was significantly lower than the third aftereffect block ($t_{261} = -6.4,\ p_{bf} < 0.001,\ d_z = -1.2$). Given that this block occurs after a set of proprioceptive probe trials, the difference here may indicate that proprioceptive trials had an attenuating effect on implicit adaptation ('t Hart and Henriques 2016).

We next assessed whether adaptation remained stable across days. While there was no main effect of Day ($F_{1,261} = 0,\ p = 1, \eta^2 = 0.04$), the Day x Block interaction was significant ($F_{4,261} = 6.3$, $p < 0.001, \eta^2 = 0.01$). Post-hoc t-tests revealed that the aftereffect was smaller on day 2 compared to day 1 in block 3 ($t_{261} = -5.1,\ p_{bf} < 0.001, d_z = 0.91$). A similar pattern was evident in the other blocks, with the magnitude of the aftereffect lower on day 2 by about 4□. This attenuation has been observed in previous studies (Avraham, Ryan Morehead, et al. 2020; Wilterson and Taylor 2019; Stark-Inbar et al. 2017; Leow et al. 2020).

Proprioceptive Shift

We then assessed whether the exposure to the rotation resulted in a proprioceptive shift, quantified as the angular change in the centroid of proprioceptive estimates, relative to the baseline. The effect of Block was significant (Figure 2.3C) ($F_{4,261} = 4,\ p = 0.003, \eta^2 = 0.27$), with a ~4° proprioceptive shift towards the rotated feedback from baseline to PB1 ($t_{261} = -3.9,\ p_{bf} = 0.005,\ d_z < -0.7$). Consistent with a previous study (Ruttle et al. 2016), the shift remained stable across successive blocks (all pairwise comparisons of successive blocks in Day 1 were not significant: $t_{261} < 0.1,\ p_{bf} = 1,\ d_z < 0.03$). In addition, the magnitude of the proprioceptive shift was stable across days, with neither the effect of Day ($F_{1,261} = 0,\ p = 1, \eta^2 = 0.004$), or significant Day x Block interaction ($F_{4,261} = 0.3,\ p = 0.84, \eta^2 = 0.004$), consistent with the findings reported by Liu et al (Liu, Sexton, and Block 2018).

Proprioceptive Variability

To operationalize proprioceptive variability, we calculated the standard deviation of the angular hand report data for each block (Figure 2.3D). There was no main effect of block ($F_{4,261} = 0.60$, $p = 0.66, \eta^2 = 0.05$). The effect of Day was significant ($F_{1,261} = 13.0,\ p < 0.001, \eta^2 = 0.08$), with proprioceptive variability reduced on day 2 compared to day 1 ($t_{261} = -4.9\ \ p_{bf} < 0.001$, $d_z = -0.9$). This between-day attenuation may be attributed to participants' increased familiarity with the proprioceptive task on day 2, leading to more consistent proprioceptive judgments (Wang et al. 2019). Nominally, proprioceptive variability was nonetheless similar across both days (~7°), with no interaction observed between Block and Day ($F_{4,261} = 1.0,\ p = 0.42, \eta^2 = 0.01$).

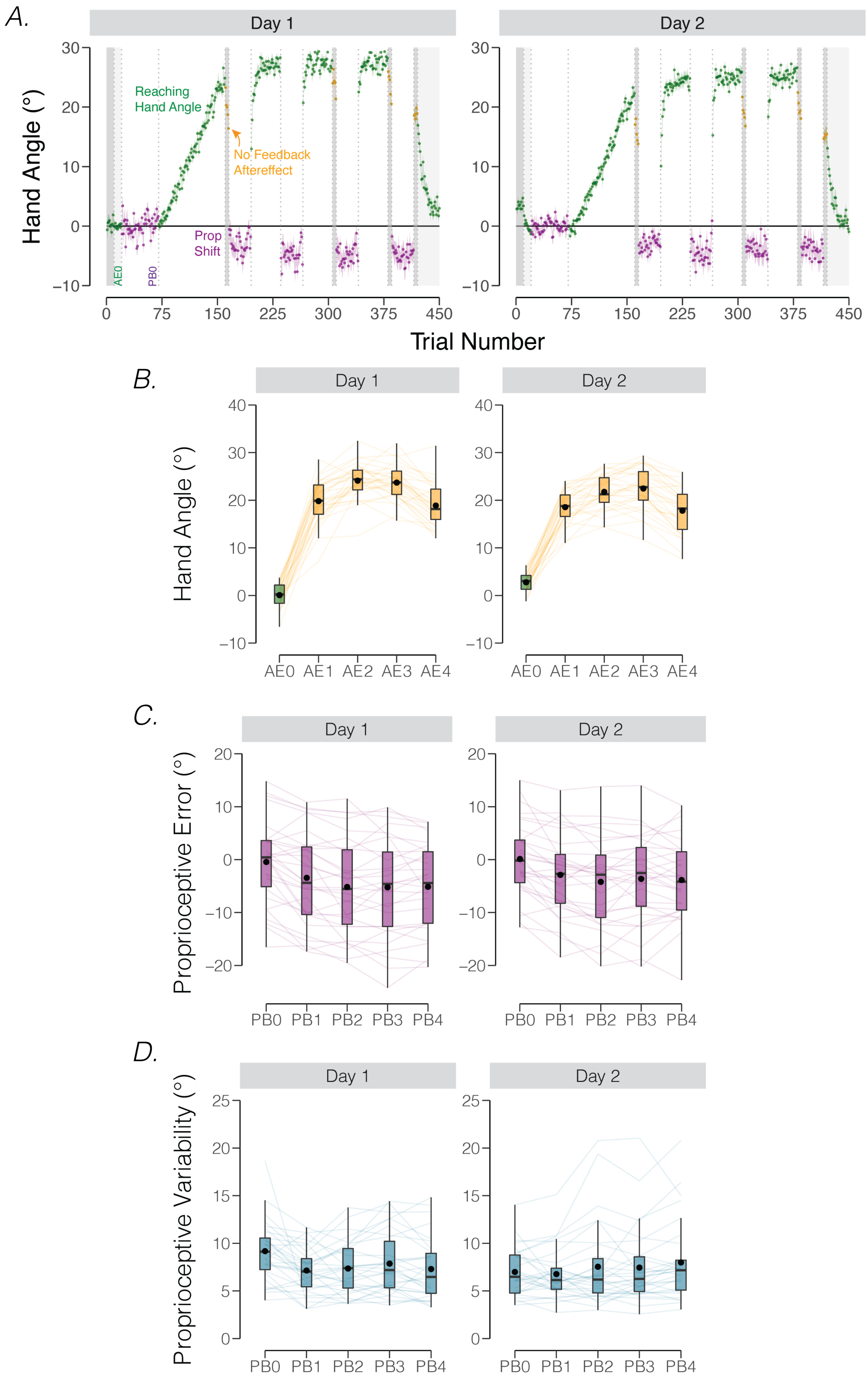

Figure 2.3. Performance on adaptation and proprioception probe tasks in experiment 1. **A)** Group means across test session (Left – Day 1, Right – Day 2). After a period of baseline trials, participants were exposed to a gradually increasing visuomotor rotation up to 30º, where it was then held constant. Participants performed blocks of visuomotor rotation trials (hand angle shown in green), no feedback aftereffect trials (hand angle shown in yellow), and proprioceptive probe trials (shift in perceived position shown in purple).

Vertical dotted lines indicate block breaks. Shaded trials indicate reaching trials either with no feedback (dark grey) or with veridical feedback (light grey). Shaded regions indicate ± SEM. Baseline blocks for reaching hand angle (AE0) and proprioceptive probes (PB0) are labeled. **B)** Hand angle during no feedback aftereffect blocks. **C)** Proprioceptive errors for each proprioceptive block. **D)** Variability of proprioceptive judgments for each proprioceptive probe block. Thin lines indicate individual subjects. Box plots indicate min, max, median, and the 1st/3rd interquartile range. Black dots indicate the mean.

Reliability of the dependent variables

Analyses which involve correlating individual differences across different measures are limited by the reliability of each measure. Thus, before turning to the correlational analyses between the proprioceptive measures and implicit adaptation, we assessed the reliability of our core measures across sessions. For adaptation, we used the mean of the last two aftereffect blocks (AE2 - AE3) given that adaptation has reached its limit by these blocks. For proprioceptive shift, we used the mean proprioceptive shift of all blocks (PB1 – PB4) after the perturbation was introduced relative to baseline. For proprioceptive reliability, we used the proprioceptive variability from all blocks (PB0 – PB4). The between-session correlations were significant for all three dependent variables (Figure 2.4A-C) (implicit adaptation: $R = 0.53, p = 0.00\ 2$; proprioceptive variability: $R = 0.59, p < 0.00\ 1$; proprioceptive shift: $R_s = 0.5, p = 0.005$), indicating that the individual differences were reasonably stable.

Correlating Adaptation and Proprioception

Having established that these dependent variables were reliable across days, we next asked whether differences in implicit adaptation could be accounted for by individual differences in proprioception. To obtain more stable measures of proprioception and implicit adaptation, we averaged the mean values for each dependent variable from day 1 and day 2.

According to the multisensory integration hypothesis, we should expect a positive correlation between proprioceptive variability and the extent of adaptation since, all other things being equal, noisier proprioception would diminish the relative weighting given the proprioceptive sensory prediction error. Consistent with this prediction, the two measures were positively correlated (Figure 2.4D: $R = 0.49,\ p = 0.006$).

According to the proprioceptive realignment hypothesis, we should expect a correlation between the proprioceptive shift and implicit adaptation. Given that these two effects should be in opposite directions, the correlation should be negative: A larger (more negative) proprioceptive shift would require a larger change in hand angle for the hand to be perceived at the target location. Consistent with the proprioceptive realignment hypothesis, there was a significant negative correlation between proprioceptive shift and aftereffect (Figure 2.4E: $R_s = -0.40,\ p = 0.03$).

We also examined the correlation between proprioceptive shift and proprioceptive variability. Although we had no strong *a priori* expectations here, a signal-dependent perspective might predict a negative correlation (Harris and Wolpert 1998) if we assume that variance grows with the magnitude of the shift. Similarly, one might suppose that the perceived location of the hand might be more malleable if the inputs underlying that judgment are more variable. However, proprioceptive variability and proprioceptive shift were not correlated (Figure 2.4F: $R = -0.13$, $p = 0.48$), an observation in line with previous work reporting the absence of a relationship between the magnitude of cross-sensory calibration and signal reliability (Zaidel, Turner, and Angelaki 2011; Ayala, Marius ’t Hart, and Henriques 2020).

Given that proprioceptive shift and proprioceptive variability were uncorrelated with each other yet both measures correlated with the upper bound of adaptation, we could test a unique prediction of the proprioceptive re-alignment model: Namely, that the upper bound of adaptation would be better predicted by a model that includes both shift and variability (Eq 2.5), compared to models that only include one of these two variables. Our multiple regression analysis was consistent with this prediction: A model that included *both* shift and variability provided the most parsimonious account of our data ($R^2_{adj} = 0.22$) relative to the two single-variable models (proprioceptive shift only: $R^2_{adj} = 0.07$; proprioceptive variability only: $R^2_{adj} = 0.21$). This analysis indicates that proprioceptive shift and variability make independent contributions towards predicting the upper bound of adaptation, providing additional support for the proprioceptive re-alignment account of sensorimotor adaptation.

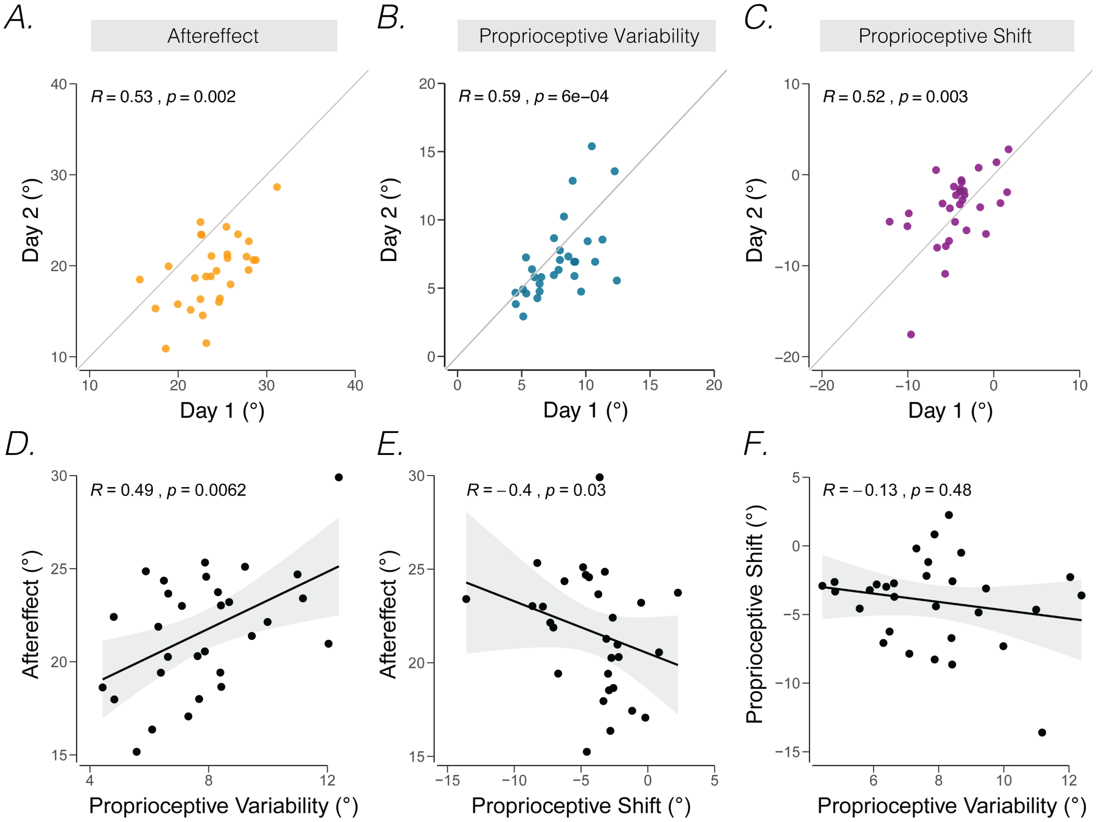

Figure 2.4. Inter-individual differences analyses in experiment 1. Test-retest reliability, measured across days for **A)** aftereffect from adaptation (yellow) **B)** proprioceptive variability (blue) and **C)** proprioceptive shift (purple). Correlations between different dependent variables: **D)** proprioceptive variability vs aftereffect; **E)** proprioceptive shift vs aftereffect; **F)** proprioceptive variability vs proprioceptive shift. Black line denotes the best fit regresion line and the shaded region indicates the 95% confidence interval.

Experiment 2

Exp 2 (n = 32) provided a second test of the multisensory integration and proprioceptive realignment hypotheses, using a visual error clamp in which the feedback cursor was always offset from the target by 15º. Compared to Exp 1 where the contingent feedback constrained the degree of adaptation, we expected the clamp to yield a greater range of values for implicit adaptation.

Implicit Adaptation

The participants' reaches shifted in the opposite direction of the error clamp feedback, the signature of implicit adaptation (Figure 2.5). The hand angle data (CB0 – CB4, using the last 90 trials of CB1, and all 90 trials in CB2 – CB4) showed a main effect of Block ($F_{4,124} = 55.1,\ p < 0.01,\ \eta^2 = 0.06$), with post-hoc comparisons indicating that the mean hand angle in each block was significantly greater than baseline (all $t_{124} > 10.75,\ p < 0.001,\ d_z > 1.9$). The mean values were not significantly different from one another for the four clamp blocks (all pairwise t-tests: $t_{124} < 2.47,\ p > 0.13,\ d_z < 0.44$), indicating that participants had reached the asymptote of adaptation by the end of the first clamp block. To obtain a single measure of adaptation for each participant, we took the mean hand angle over the last three clamped feedback blocks. The mean change in hand angle was 17.5º ± 13.9º. As expected, the range of asymptotic values was considerably larger in Exp 2 (range = -6.5º – 58.5º) compared to Exp 1 (range = 13.5º – 33.9º).

Proprioceptive Measures

The proprioceptive shift in Exp 2 was modest, and only marginally significant ($F_{4,124} = 2.17$, $p = 0.08,\ \eta^2 = 0.06$). The mean value was -1.2° (SD = 11.4°), less than 33% of the -4.0° (SD = 3.2°) mean shift observed in Exp 1 ($t_{59} = -4.3,\ p < 0.001,\ d = -1.1$). 12 of the 32 participants exhibited a shift in the direction opposite to the cursor (compared to 2 out of 30 in Exp 1). Not only was the between-subject variability larger in Exp 2, but we also observed a large increase in within-subject proprioceptive variability (Exp 1, day 1: 7.8 ± 0.4 °, range = 4.4 – 12.4, Exp 2: 11.2 ± 1.0, range = 4.5 – 23.7; $t_{60} = 3.1,\ p = 0.003,\ d = 0.8$).

While we will consider these unexpected differences in detail in the Supplemental Discussion section, we note here that the large increase in the variability of the proprioceptive judgments is especially puzzling given that the two experimental protocols are very similar. It is possible that the clamped, non-contingent feedback used in Exp 2 has a different impact on sensed hand position compared to the contingent feedback provided in Exp 1 (see Supplemental Discussion: *Between-experiment analysis of the proprioceptive re-alignment integration*). Alternatively, it may be related to other methodological differences. In particular, the studies were run by different experimenters, and they may have differed in how they passively displaced the participant's arm, perhaps moving at different speeds.

Nonetheless, the proprioceptive shift and proprioceptive variability scores remained relatively stable across Exp 2. As noted above, in terms of mean values, there was no effect of block for proprioceptive shift. There was also no effect of block on proprioceptive variability ($F_{4,124} = 1.1$, $p = 0.34,\ \eta^2 = 0.04$). More important in terms of the correlational analyses reported below, individual differences were maintained across the blocks for both proprioceptive shift (all pairwise correlations following the introduction of clamped feedback, from PB1 – PB4: $R > 0.87,\ p < 0.001$) and proprioceptive variability (all pairwise correlations between PB0 – PB4: $R > 0.76$, $p < 0.001$).

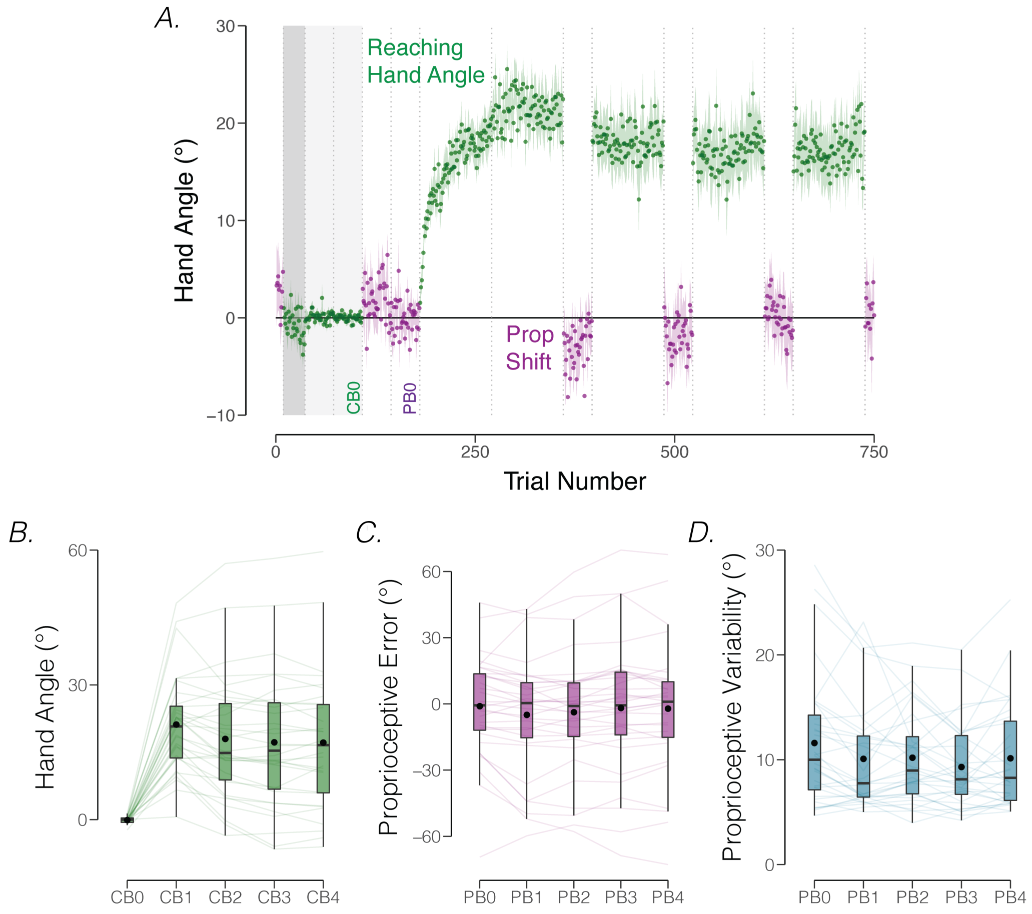

Figure 2.5. Performance on adaptation and proprioception probe tasks in experiment 2. **A)** Group means across test session. After a period of no feedback (dark grey region) and veridical feedback (light grey region) baseline trials, participants were exposed to a visual clamp in which the feedback was offset by 15º from the target. Participants performed blocks of reaching trials (hand angle shown in green) and proprioceptive probe trials (shift in perceived position shown in purple). Vertical dotted lines indicate block breaks. Shaded regions indicate ± SEM. Baseline blocks for reaching hand angle (CB0) and proprioceptive probes (PB0) are labeled. **B)** Mean hand angle averaged over the last three clamped feedback blocks. **C)** Proprioceptive error for each proprioceptive block. **D)** Variability of proprioceptive judgments for each proprioceptive probe block. Thin lines indicate individual subjects. Box plots indicate min, max, median, and the 1st/3rd interquartile range. Black dots indicate the mean.

Correlating Adaptation and Proprioception

The correlational analysis between the three dependent variables yielded a similar pattern as that observed in Exp 1 (Figure 2.6). Consistent with the multisensory integration hypothesis, there was a positive correlation between the asymptote of implicit adaptation and proprioceptive variability ($R = 0.39, p = 0.026$). Consistent with the proprioceptive realignment hypothesis, there was a negative correlation between the asymptote of adaptation and the magnitude of proprioceptive shift ($R = -0.62$, $p < 0.001$). There was no correlation between proprioceptive shift and proprioceptive variability ($R = -0.007, p = 0.97$).

We note that the correlations with the proprioceptive shift must be qualified. First, the net effect of proprioceptive shift was only marginally significant. Second, there were extreme values in both directions, including participants who showed a large shift in the opposite direction of the expected shift (i.e., away from the clamped feedback). To provide more conservative estimates, we repeated the correlational analyses after applying various inclusion criteria: 1) Limited to participants who showed the expected negative shift (Figure 2.6B; N = 20, $R = -0.70, p < 0.001$); 2) Excluding those with a shift >10° in the unexpected direction (N = 28, $R = -0.72, p < 0.001$); 3) Excluding those showing a shift >10° in either direction (N = 23, $R = -0.48, p = 0.02$); 4) Only using the proprioceptive shift data from the first block where proprioceptive shifts are most pronounced ($R = -0.61, p < 0.001$); and 5) using a more conservative, non-parametric Spearman correlation (N = 32, $R_s = -0.57, p < 0.001$). The correlation, in all cases, remained significant, pointing to a robust relationship between proprioceptive shift (albeit small) and implicit adaptation.

Consistent with Experiment 1, the multiple regression analysis also favored the proprioceptive re-alignment model. The model with both proprioceptive shift and variability ($R^2_{adj} = 0.50$) was superior to models that only included one variable (proprioceptive shift only: $R^2_{adj} = 0.36$; proprioceptive variability only: $R^2_{adj} = 0.12$). This result again points to the relevance of both bias and variability measures of proprioception on sensorimotor adaptation.

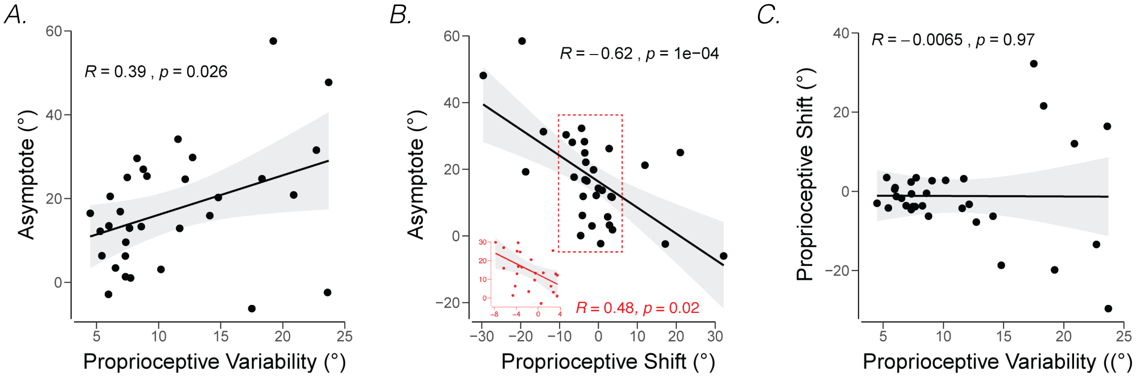

Figure 2.6. Inter-individual differences analyses in experiment 2. **A)** Proprioceptive variability vs asymptote in response to the visual clamp. **B)** Proprioceptive shift vs asymptote. A second correlation was performed on non-outlier data points contained in the red rectangle, also shown in the inset. **C)** Proprioceptive variability vs proprioceptive shift. Black line denotes the best fit regresion line and the shaded region indicates the 95% confidence interval.

Discussion

The sensorimotor system uses visual and proprioceptive feedback to remain properly calibrated. Recent sensorimotor adaptation studies using visual perturbations to induce recalibration have revealed an upper bound on this process, beyond which changes in performance require alternative learning processes. While the contribution of vision to adaptation has been well characterized (Burge, Ernst, and Banks 2008; Ernst and Banks 2002; Robert J. van Beers 2012; Wei and Körding 2010), the contribution of proprioception to adaptation remains poorly understood. Here, we took an individual differences approach, asking whether the extent of adaptation is correlated with biases and/or variability in the perceived position of the hand during adaptation.

There were two key findings: First, participants with greater proprioceptive variability in both experiments exhibited more implicit adaptation, a finding consistent with the multisensory integration account (Burge, Ernst, and Banks 2008; Ernst and Banks 2002; Robert J. van Beers

2012; Wei and Körding 2010). The asymptotic level of adaptation, in this view, reflects an equilibrium between learning from visual and proprioceptive error signals. This finding is consistent with adaptation being driven by the optimal weighting of proprioception and vision according to their relative variability, whereby greater proprioceptive variability results in greater weighting of visual feedback, and thus greater implicit adaptation. Second, participants with larger proprioceptive shifts towards the visual feedback exhibited larger implicit adaptation, a finding consistent with the proprioceptive realignment hypothesis (Salomonczyk, Cressman, and Henriques 2013; Cressman and Henriques 2010, 2009; Ruttle, Hart, and Henriques 2020; Rossi, Bastian, and Therrien 2021). The multiple regression analysis in each experiment provided further support for the proprioceptive realignment model, highlighting the impact of both the bias and variability in sensed hand position in modulated sensorimotor adaptation (Eq 2.5). The asymptotic level of adaptation, in this view, reflects the point of realignment between the sensed hand position and the target.

We note that our focus on how asymptotic performance might arise from the integration of multisensory cues is somewhat orthogonal to the dominant account in the literature of this phenomenon. The core idea emphasized in the literature is that the asymptote reflects the point of equilibrium between learning and forgetting processes (Smith, Ghazizadeh, and Shadmehr 2006; Albert et al. 2019; Kording, Tenenbaum, and Shadmehr 2007; Donchin, Francis, and Shadmehr 2003; Thoroughman and Shadmehr 2000), an idea captured in the standard state-space model. This model in its basic form does not specify the sources of information driving learning, although in most applications, the visual (or task) error is treated as the sole contributor to learning. As such, the state-space model does not readily yield predictions concerning the relationship between measures of proprioception and adaptation. The two hypotheses featured here could be taken to extend the conventional notion of learning and forgetting, specifying sensory constraints on both these processes. Rather than assuming that visual errors are the sole contributor of learning, we highlight important proprioceptive constraints on adaptation.

Proprioceptive variability and asymptotic adaptation

Greater proprioceptive variability predicted a greater asymptotic magnitude of implicit adaptation. While we are unaware of any prior reports of this positive correlation, a recent study asked a related question: Does proprioceptive variability predict the early learning rate in response to the abrupt introduction of a 30° visuomotor rotation (Lei and Wang 2018). This study reported no correlation between proprioceptive variability and early learning in young adults and a negative correlation in older adults. While these observations may appear inconsistent with the results of our study, their main dependent variable, early learning, likely reflects a strong contribution from explicit processes in response to this large perturbation (Bond and Taylor 2015; A. M. Haith, Huberdeau, and Krakauer 2015; Werner et al. 2015), rather than implicit adaptation. By this view, the null result for the young adults would suggest that proprioceptive variability is not related to explicit learning, whereas the negative correlation observed in older adults may reflect a concurrent age-dependent deterioration of strategy use and proprioceptive acuity (Vandevoorde and Orban de Xivry 2019). Interestingly, older adults have also been shown to exhibit an age-dependent boost in implicit adaptation (Vandevoorde and Orban de Xivry 2019). By the multisensory integration hypothesis, this increase would be expected if a decline in proprioceptive sensitivity is accompanied by an increase in proprioceptive variability, a hypothesis that can be tested using an individual difference approach in an older adult sample.

Previous tests of the multisensory integration account of implicit adaptation have focused exclusively on manipulations of the visual feedback. Increasing visual variability, either by replacing a small cursor with a cloud of dots or a Gaussian blur, has been shown to decrease the rate and extent of implicit adaptation (Wei and Körding 2010; Burge, Ernst, and Banks 2008;

Jonathan S. Tsay, Avraham, et al. 2021). Surprisingly, the sensory integration models put forth to account for these effects have not measured proprioception; rather, this component has either been estimated as a free parameter or ignored entirely. Here we obtained direct measures of proprioceptive variability to test a core prediction of the multisensory integration model. A limitation with our individual difference approach, however, is that the analyses are purely correlational (for further discussion on this point, see the Supplemental Discussion section: *Addressing concerns with correlational analyses*). Future studies using experimental methods to perturb proprioception (e.g., tendon vibration) (Goodwin, McCloskey, and Matthews 1972; Gilhodes, Roll, and Tardy-Gervet 1986; J. P. Roll, Gilhodes, and Tardy-Gervet 1980; Manzone and Tremblay 2020; Bernier et al. 2007) could build on our results, asking whether proprioceptive variability has a causal role in modulating the upper bound of adaptation.

One prediction of the multisensory integration hypothesis is that the magnitude of the asymptote will be related to the size of the visual SPE. This holds up to the point where the adaptation response saturates, estimated to be between 6° and 20° (Wei and Körding 2009; Kim et al. 2018). Whereas the SPE in Exp 1 is ~3° (estimated from late adaptation), it is fixed at 15° in Exp 2; as such, the multisensory integration hypothesis would predict a much larger asymptote in Exp 2 to yield the proprioceptive SPE required to produce an equilibrium. At odds with this prediction, the asymptotes were similar (~20°). From Eq 2.2, there are two ways in which a similar asymptote could occur despite a five-fold difference in visual SPE between experiments. First, proprioceptive variability could be smaller in Exp 2 to increase the weight given to proprioception. Our data are inconsistent with this hypothesis, with the trend showing slightly greater proprioceptive variability in Exp 2. Alternatively, an increase in visual variability in Exp 2 would lead to a similar increase in the weight given to proprioception. This seems plausible. More attention is likely directed to the task relevant, contingent cursor in Exp 1 compared to the task irrelevant, non-contingent cursor in Exp 2 (a point emphasized by the instructions). Moreover, the smaller visual SPE in Exp 1 is likely more foveal that the larger visual SPE in Exp 2. Given that visual attention and visual eccentricity modulate visual variability (Limanowski and Friston 2020; Carrasco, Williams, and Yeshurun 2002; Yeshurun and Carrasco 1998), it is plausible that visual variability was higher in Exp 2 (see Supplemental Discussion section: *Between-experiment analysis of the multisensory integration hypothesis*).

Proprioceptive shifts and asymptotic adaptation

In line with the proprioceptive realignment hypothesis, the upper bound of implicit adaptation was also correlated with the proprioceptive shift induced by the visual perturbation: Larger shifts were associated with (a negative correlation because of the direction used to measure the shift). The proprioception realignment hypothesis offers an alternative multisensory integration perspective on adaptation, albeit one that entails *two* distinct processes. One process involves the optimal estimate of hand position *without* the influence of vision, an estimate assumed to be influenced by a prior (i.e., the target location) and the actual hand position. The other process is driven by vision, the biased sense of hand position arises with the introduction of the perturbed visual feedback, the proprioceptive shift. While the exact computational rules that govern proprioceptive shifts remain an active area of research, the size of the shift presumably depends on the size of the visual feedback ((’t Hart, Ruttle, and Henriques 2020). The sum of these two signals defines the error signal that drives adaptation. Thus, as the hand adapts in the opposite direction of the target, the signal from the actual hand position can eventually negate the (stable) proprioceptive shift. The current results would suggest that the proprioceptive shift is given much more weight than the actual hand position: In the group means, a proprioceptive shift of ~3° is only offset when the hand has adapted to around ~20°.

Verbal reports of sensed hand position obtained in a continuous manner *during* adaptation provide converging evidence of the dynamics predicted by the proprioceptive realignment hypothesis. The report data followed a striking non-monotonic function, initially biased towards the clamped cursor (away from the target), and then reversing direction (Jonathan Sanching Tsay, Parvin, and Ivry 2020). However, the asymptotic value of the reports was not at the target. Rather, it was shifted slightly away from the target in the opposite direction of the clamp. This "overshoot" is not predicted by either the multisensory integration or proprioceptive realignment hypotheses, a puzzle that remains to be addressed in future research.

While proprioceptive shift and implicit adaptation were negatively correlated in both experiments, the net effect of proprioceptive shift was considerably greater in Exp 1 (~5°) compared to Exp 2 (~1°). In a post-hoc comparison across experiments, we noted a striking difference between subgroups exposed to a CW perturbation compared to those exposed to a CCW perturbation. For those exposed to a CW perturbation, the results were quite similar across experiments groups (Exp 1: -5.1 ± 0.6 and Exp 2: -5.4 ± 2.7, both shifted towards the visual cursor). However, for those exposed to a CCW perturbation, the proprioceptive shifts were quite different. In Exp 1, the shift was in the expected direction, towards the visual cursor (3.0 ± 0.9°). In contrast, in Exp 2, the shift was in the opposed direction, away from the visual cursor (-3.0 ± 2.7). The source of this difference and in particular, the highly atypical result for the CCW subgroup in Exp 2 is unclear. It may reflect measurement noise — the proprioceptive data were much nosier in Exp 2. Alternatively, our measure of proprioceptive shift may conflate two types of proprioceptive changes: A change in proprioception due to the visual signal and a change in proprioception within the proprioceptive system itself. A number of studies had described the phenomenon of proprioceptive drift, a shift in perceived hand position with repeated reaches ((Wann and Ibrahim 1992; Brown, Rosenbaum, and Sainburg 2003a). The relative contribution of visually induced proprioceptive shifts and proprioceptive drift may differ across these two experiments, perhaps related to the difference in how the system responds to a contingent and non-contingent feedback signal. (See an extended discussion of this speculative hypothesis in the Supplemental Discussion: *Between-experiment analysis of the proprioceptive re-alignment integration*).

Reconciling multisensory and proprioceptive realignment hypotheses

The core predictions for both the multisensory integration and proprioceptive realignment hypotheses were confirmed in the present experiments. The proprioceptive realignment model, in its current form, seems to provide a more parsimonious explanation, as it predicts implicit adaptation to be correlated with both proprioceptive shift and variability. However, our findings do not rule out the possibility that both hypotheses, one based on the variability of proprioception and the other based on the shift in proprioception, operate in parallel manner. The absence of a correlation between the two proprioceptive measures, a finding consistent with several previous reports (H. J. Block and Bastian 2011; Zaidel, Turner, and Angelaki 2011; Cressman and Henriques 2009; Izawa, Criscimagna-Hemminger, and Shadmehr 2012), is consistent with a dual-process model (see also, (H. J. Block and Bastian 2011). By this view, the observed asymptote is a composite of these two forms of adaptation. That is, a ~20º asymptote is actually an equilibrium point between one process that weights the visual and proprioceptive inputs and a second process that seeks to counteract the proprioceptive shift.

Alternatively, there may be a more complex interaction between processes sensitive to proprioceptive variability and bias. We could envision a multi-stage process in which a reliability weighting rule for each sensory signal operates at an early stage, with the integration of the multiple signals occurring at a later stage (perhaps in a non-weighted manner)Examples of the former are found in the optimal integration literature (Takahashi, Diedrichsen, and Watt 2009; Shams and Beierholm 2010; Körding et al. 2007; Wei and Körding 2009). Examples of the latter are also ubiquitous, where proprioception and vision interact in a fixed manner, independent of variability (Zaidel, Turner, and Angelaki 2011; Zaidel, Ma, and Angelaki 2013; M. K. Rand and Heuer 2019; M. Rand and Heuer 2020). These stages of processing result in a final error signal, one that ultimately drives motor adaptation. While these ideas remain to be fleshed out in future research, the current results underscore the critical role of proprioception in sensorimotor adaptation.

Supplemental Discussion

When people adapt to a visual perturbation, implicit adaptation reaches an asymptote. The multisensory integration hypothesis predicts that the asymptote is positively correlated with proprioceptive variability (Eq. 2.2), whereas the proprioceptive re-alignment hypothesis predicts that the asymptote is negatively correlated with proprioceptive shift (Eq 2.5). In the main paper, we evaluate these hypotheses *within each experiment*. In the following discussion, we consider differences *between the two experiments* and how these bear on the two hypotheses.

To highlight between-experiment differences, Table 2.1 summarizes the empirical and derived parameters from each experiment, with the latter obtained by inserting the group mean values into the relevant equations in the manuscript: 1) Under the multisensory integration hypothesis, visual variability is derived by using the empirically observed values for proprioceptive variability and asymptote into Eq 2.2. 2) Under the proprioceptive re-alignment hypothesis, prior variability of hand location is derived by using the empirically observed values for proprioceptive shift, proprioceptive variability, and asymptote into Eq 2.5. Note that this simple approach does not provide an estimate of confidence intervals for the derived values, something that could be obtained with estimation methods such as bootstrapping. However, the derivations are meant as a heuristic, helping highlight issues that may require modifications of the two hypotheses concerning how proprioception contributes to asymptotic performance.

Table 2.1	Empirical (Means)				Derived	
	Prop Var (σ^2_{prop})	Prop Shift (PS)	Asymptote ($\mu_{prop,UB}$)	Visual SPE (μ_{vis})	Visual Var (σ^2_{vis})	Prior Var (σ^2_{prior})
Exp 1	7.8	-4.0	21.6	3	1.1	1.8
Exp 2	11.2	-1.2	17.5	15	9.6	0.8

Between-experiment analysis of the multisensory integration hypothesis

The cursor feedback in Exp 2 provided a larger visual SPE (15°) compared to that of Exp 1 (~3°, estimated during late adaptation when hand angle has saturated). If visual and proprioceptive variance were the same in the two experiments, then we should expect a higher asymptote in Exp 2, a prediction that is inconsistent with the observed results. While this could, of course, be reason to question the model, it is also useful to consider that the sensory variances may not be the same in the two experiments.

We can use the empirical values from Exp 1 to predict the asymptote for Exp 2, given the increase in visual SPE. Using our empirical estimates of proprioceptive variability ($\sigma^2_{prop} = 7.8°$) and asymptote ($\mu_{prop,UB} = 21.6°$) in Exp 1, we obtain the estimate of visual uncertainty (Eq. 2.3 in the manuscript):

$$21.6 = \frac{7.8}{\sigma^2_{vis}} * 3 \qquad 2.6$$

2.7 $$\sigma_{vis}^2 = 1.1$$

Note that this estimate of σ_{vis}^2 is consistent with the idea that visual uncertainty is, in general, significantly less than proprioceptive uncertainty (R. J. van Beers, Sittig, and Denier van der Gon 1998; Robert J. van Beers, Wolpert, and Haggard 2002; Sober and Sabes 2003).

Under the assumption that sensory variances (σ_{vis}^2 and σ_{prop}^2) are the same across experiments, we can estimate the asymptotic value, $\mu_{prop,UB}$, for Exp 2:

2.8 $$\mu_{prop,UB} = \frac{7.8}{1.1} * 15$$

2.9 $$\mu_{prop,UB} = 106.4$$

This results in an absurdly large asymptote (106.4°), far from the empirically measured values (17.5°). The predicted asymptote is even larger (152.7°) if we use the empirically measured proprioceptive variability in Exp 2 (11.2°).

However, there are several reasons to question the assumption that visual uncertainty should be the same in Exps 1 and 2. First is the relevance of the visual cursor. In Exp 1, the cursor is relevant, with participants instructed to reach so that the cursor intersects the target. In contrast, participants are told that the cursor is irrelevant in Exp 2 and instructed to ignore it. Second, the visual eccentricity of the cursor is greater in Exp 2 compared to Exp 1. Given that visual attention and eccentricity impact visual acuity (Yeshurun and Carrasco 1998; Limanowski and Friston 2020; Carrasco, Williams, and Yeshurun 2002), it is reasonable to assume that visual uncertainty will be higher in Exp 2.

We can use the multisensory integration model as a way to assess the change in visual uncertainty required to produce the asymptotic differences. Below, we derive visual uncertainty in Exp 2 using empirical estimates of asymptote ($\mu_{prop,UB} = 17.5°$), proprioceptive variability ($\sigma_{prop}^2 = 11.2°$), and the visual error size ($\mu_{vis} = 15°$):

2.10 $$17.5 = \frac{11.2}{\sigma_{vis}^2} * 15$$

2.11 $$\sigma_{vis}^2 = 9.6°$$

As can be seen in Eq 2.11, the derived value of visual uncertainty in Exp 2 is 9.6°, a value that is much larger than the derived value of 1.1° for Exp 1, consistent with the expectation that σ_{vis}^2 would be greater when visual feedback is ignored and positioned at a larger eccentricity.

Instead of considering differences in visual uncertainty between the experiments, we could consider differences in proprioceptive variability between experiments. *A priori*, we would expect no difference since the method for measuring proprioceptive variability is nearly identical between experiments. Nonetheless, the group means show a difference (Table 2.1) with proprioceptive variability being greater in Exp 2. While this could well be measurement noise, we note that the data for Exps 1 and 2 were collected by different experimenters (one per experiment). Perhaps subtle methodological differences (e.g., passively displacing the participant's arm at different speeds) may have driven this difference. Critically, however, greater proprioceptive variability in Exp 2 would predict a greater asymptote in Exp 2 under the multisensory integration hypothesis (Eq 2.3), a prediction which is inconsistent with our data.

Together, these derivations suggest one viable explanation for the asymptotic differences between experiments based on the multisensory integration hypothesis, namely that visual uncertainty is greater in Exp 2 compared to Exp 1.

Between-experiment analysis of the proprioceptive re-alignment integration

Perhaps the biggest puzzle in our results is the finding that proprioceptive shift was, on average, much smaller in Exp 2 compared to Exp 1 (4°) (see Table 2.1). Whereas the 4° value for Exp 1 is in accord with the literature (Cressman and Henriques 2011), the 1° value for Exp 2 is surprisingly low. Moreover, whereas the mean values for proprioceptive shift remained relatively constant across the probe blocks in Exp 1, these values were reduced across the probe blocks in Exp 2, starting at a mean value of -3° and reaching a mean value of -1° in the last probe block. These observations led us to take a closer look at the data. One interesting, and unexpected post-hoc observation was revealed when we divided the data by participants who experienced either a CW or CCW rotation (Table 2.2).

Table 2	Perturbation Direction	Proprioception				Motor	
		Variance Mean (SEM)		Shift Mean (SEM)		Upper Bound Mean (SEM)	
Exp 1	CW (-)	7.9	(0.5)	-5.1	(0.6)	22.0	(0.6)
	CCW (+)	7.8	(0.6)	3.0	(0.9)	-21.3	(1.0)
Exp 2	CW (-)	11.9	(1.7)	-5.4	(2.7)	21.2	(4.2)
	CCW (+)	10.5	(1.2)	-3.0	(2.7)	-13.5	(2.6)

Between experiments, the means for proprioceptive shift and asymptote were similar for the CW groups. However, there was a marked difference between experiments for the CCW groups. In Exp 1, the proprioceptive shift was *towards* the visual cursor (CCW direction) by 3° and the adaptive response was around 21° *away* from the visual feedback, effects that were both in the expected direction. A different pattern was seen in Exp 2. Here the proprioceptive shift was in the unexpected direction, now shifted *away* from the visual cursor (in the CW direction). The asymptote remained in the expected direction, *away* from the visual feedback, but the magnitude of the asymptote was only 13°, a reduction of over 30% from that observed in the other three conditions (~21°).

Beyond these numeric differences, the finding that the proprioceptive shift is in the unexpected direction is a major problem for the proprioceptive re-alignment model since this model would predict that adaptation should now have also occurred in the unexpected direction, that is towards the cursor.

At present, we can only offer two non-mutually exclusive hypotheses about how the proprioceptive re-alignment model might accommodate the overall pattern since in the two experiments when considering the differences between the CW and CCW groups. First, the proprioceptive shifts in the CCW group in Exp 2 may reflect measurement noise. The possibility that measurement noise is high in this experiment is consistent with the relatively large SEM for proprioceptive shifts in this group (Table 2.1). Perhaps due to random sampling, we ended up with less motivated and meticulous participants in the CCW group in Exp 2, compared to the CW group.

To estimate the amount of measurement noise, we used the CW group in Exp 2 to derive an estimate of σ^2_{prior}.

2.12 $$21.2 = 5 * \frac{\sigma^2_{prior} + 11.9}{\sigma^2_{prior}}$$

2.13 $$\sigma^2_{prior} = 3.6$$

The derived value of σ^2_{prior} combined with the empirical values of proprioceptive shift and variability for the CW group, allow us to estimate how much proprioceptive shift would be necessary to achieve 13.5° of adaptation:

2.14 $$PS = \frac{-\mu_{prop,UB} * \sigma^2_{prop}}{\sigma^2_{prior} + \sigma^2_{prop}}$$

2.15 $$PS = \frac{13.5 * 3.6}{3.6 + 10.5}$$

2.16 $$PS = 3.4°$$

By this analysis of measurement noise, our obtained proprioceptive shift of -3.0° is off by 6.4° from the "true" value (3.4°).

Alternatively, the difference between the CW and CCW groups in Exp 2 might be related to another phenomenon, proprioceptive drift. Prior work has shown that one's sense of proprioception during static probes slowly drifts in the rightward direction for right-handers (i.e., CW direction for targets in the upper workspace; see (Brown, Rosenbaum, and Sainburg 2003a; Wang et al. 2020). As such, our measure of proprioceptive shift (as well as those frequently employed in the literature) may not be a pure measure of the cross-sensory influence of vision on proprioception (PS_{vis}), an effect always in the direction of the cursor, but also reflects a change in proprioception due to systematic drift (PS_{drift}) in the CW direction (given that our participants were right handers). This can be formalized as:

2.17 $$PS_{total} = PS_{vis} + PS_{drift}$$

In both experiments, CW perturbations were associated with greater total proprioceptive shifts compared to CW perturbations. This would be expected given the directional change associated with the two components: For CW perturbations, PS_{vis} and PS_{drift} are both in the CW direction; for CCW perturbations, PS_{vis} and PS_{drift} are in opposing directions. From the groups means for the CCW groups, Eq S12 would suggest that PS_{vis} was greater than PS_{drift} in Exp 1, whereas PS_{vis} was less than PS_{drift} in Exp 2.

This still begs the critical question for the proprioceptive re-alignment hypothesis: Why would adaptation be in the direction opposite to the CCW visual cursor (standard direction) if the total proprioceptive shift is shifted away from the CCW visual cursor. While admittedly speculative, one solution to this conundrum is to posit that the motor system treats the visually-induced proprioceptive shift and proprioceptive drift differently. In this account, our initial equation can be modified to include a weighting term, η, signifying the relative contribution of these two types of proprioceptive changes to the upper bound of adaptation:

2.18
$$\mu_{prop,UB} = -[\eta PS_{vis} + (1 - \eta)PS_{drift}] * \frac{\sigma^2_{prior} + \sigma^2_{prop}}{\sigma^2_{prior}}$$

When η is 1, adaptation is driven solely by PS_{vis}; when η is 0, adaptation is driven solely by PS_{drift}. By this variant of the proprioceptive re-alignment hypothesis, we would assume that adaptation is driven more by PS_{vis}. That is, despite PS_{total} in the CCW group being shifted 3° CCW (*away* from the visual clamp), adaptation from proprioceptive misalignment is in the direction away from the clamped feedback because the driving signal for adaptation is from PS_{vis} , a phenomenon that is always *towards* the clamp (but masked in PS_{total} by the effect of PS_{drift} in the CW direction).

If we assume that 1) PS_{drift} does not vary with the direction of perturbation and 2) that PS_{drift} is equal in magnitude in CW and CCW directions, we can derive PS_{drift} and PS_{vis} by solving the following system of equations with two equations and two unknowns (based on Eq 2.18):

2.19
$$CW: PS_{total} = -5.4 = PS_{vis} + PS_{drift}$$

2.20
$$CCW: PS_{total} = -3 = -PS_{vis} + PS_{drift}$$

2.21
$$PS_{drift} = -4.2; \; PS_{vis} = -1$$

The -4.2 estimate of PS_{drift} is in the CW direction and the -1 estimate of PS_{vis} is towards the visual perturbation, directions consistent with the literature (Cressman and Henriques 2011). We can use these two values to derive η, the weighting parameter (whether larger values indicate conditions in which the motor system relies on PS_{vis}), and σ^2_{prop}, an estimate of the certainly that one's prior belief of hand position is centered at the target ($\sigma^2_{prior}$is presumably very close to 0). We again have a system of equations, with two equations and two unknowns (Eq 2.18, using the empirical values from Table 2.1 for the asymptote of adaptation, $\mu_{prop,UB}$, and proprioceptive variance, σ^2_{prop}):

2.22
$$CW: 21.2 = -[\eta * -1 + (1 - \eta) * -4.2] * \frac{\sigma^2_{prior} + 11.9}{\sigma^2_{prior}}$$

2.23

$$CCW: -13.5 = -[\eta * 1 + (1 - \eta) * -4.2] * \frac{\sigma_{prior}^2 + 10.5}{\sigma_{prior}^2}$$

2.24 $$\eta = 0.96, \sigma_{prior}^2 = 0.66$$

Given that the estimate of η is close to 1, this analysis is consistent with the hypothesis that adaptation is almost exclusively driven by PS_{vis} and is essentially impervious to PS_{drift}. Through our derivation, the estimate of σ_{prior}^2 is small (relative to the sensory variances) indicating that there is a strong prior that the reach will terminate near the target.

An alternative, model-free way to reduce impact of proprioceptive drift on our correlational analyses is to focus on just the first probe block (PB1), the timepoint at which proprioceptive drift should have its weakest contribution to PS_{total}. If we use the mean value for PB1 as a measure of relatively uncontaminated PS (or as a proxy of PS_{vis} in the modified version of the model summarized in Eq 2.18), the correlation between proprioceptive shift and late adaptation is R = -0.61 ($p < 0.001$).

This admittedly complex line of reasoning provides a potential explanation for why proprioceptive shifts can occur in the unexpected direction (i.e., away from the visual cursor), yet adaptation still ensues in the expected direction (i.e., away from the visual cursor). This line of reasoning is built on the assumption that our current measure of proprioceptive shift (as well as others in the literature) may be a contaminated measure that fails to isolate the shift due to cross-sensory calibration from visual feedback on proprioceptive feedback from gradual, systematic drifts in proprioception over repeated reaches. Future studies should be able to isolate the effects of proprioceptive drift on adaptation by interleaving proprioceptive probe blocks with reaching blocks with no cursor feedback. As such, the proprioceptive probes would solely reflect the contribution of proprioceptive drift since no visual input is provided to calibrate proprioception. Moreover, the modified proprioceptive re-alignment hypothesis would predict a correlation between the amount of proprioceptive drift and the change in motor output in the absence of visual feedback.

We note that this CW and CCW difference cannot be easily explained using a traditional state space model with learning and forgetting, unless a relatively ad-hoc constraint is placed on the learning rate or forgetting rate that varies as a function of direction.

The preceding discussion focuses on how the data in Exp 2 point to the need for a modified of the proprioceptive re-alignment model, one that considers the effect of proprioceptive drift. Can this line of reasoning also be applied to reconcile why the total proprioceptive shift differs between experiments, with the shift greater in Exp 1 compared to Exp 2 (see Table 2.1)?

To tackle this issue, we first decomposed the empirically measured PS_{total} into PS_{vis} and PS_{drift} components with two equations and two unknowns from Exp 1 (identical to the method applied for Exp 2 with Eq 2.19 – Eq 2.21):

2.25 $$CW: PS_{total} = -5.1 = PS_{vis} + PS_{drift}$$

2.26 $$CCW: PS_{total} = 3 = -PS_{vis} + PS_{drift}$$

2.27 $$PS_{drift} = -1.05;\ PS_{vis} = \pm 4.05$$

Similar to the previous section (Eq 2.22 – Eq 2.24), we then solve for η and σ^2_{prop}.

2.28 $$CW: 22 = -[\eta * -4.05 + (1 - \eta) * -1.05] * \frac{\sigma^2_{prior} + 7.9}{\sigma^2_{prior}}$$

2.29 $$CCW: -21.3 = -[\eta * 4.05 + (1 - \eta) * -1.05] * \frac{\sigma^2_{prior} + 7.8}{\sigma^2_{prior}}$$

2.30 $$\eta = 0.99, \sigma^2_{prior} = 1.77$$

The results for the two experiments can be summarized as:

Table 2.3	**Exp 1**	**Exp 2**
$\boldsymbol{PS_{vis}}$	-4.05	-1
$\boldsymbol{\eta}$	0.99	0.96
$\boldsymbol{\sigma^2_{prior}}$	1.77	0.66
$\boldsymbol{PS_{drift}}$	-1.05	-4.2

These values were derived under the assumption that PS_{vis} is constant for both CW and CCW directions, as assumption that may not be true. Furthermore, without confidence intervals, it is not sensible to make inferences about effect sizes. For the sake of simplicity, we assume that these parameter values reflect population effects and discuss them in terms of their ordinal relationship between experiments, rather than in terms of exact values.

From Table 2.3, we see four main differences between the experiments:

#1 PS_{vis}: E1 > E2

#2 η : E1 >= E2

#3 σ^2_{prior}: E1 > E2

#4 PS_{drift}: E1 < E2

Differences #1 - #3 likely stem from the same source: The relevance of the visual cursor (see above, *Between-experiment analysis of the multisensory integration hypothesis*). It would seem reasonable to assume that the more relevant cursor in Exp 1, being gradually offset from the hand position, would induce a greater PS_{vis} (#1) and prompt the motor system to rely more heavily on this visually-calibrated proprioceptive signal (#2). The cursor, being contingent on hand position but offset from the target, may have also increased uncertainty about the prior associated with hand position (#3).

More puzzling is why PS_{drift} would differ between experiments (#4). We do not have a ready answer to offer. One idea is that there may be a saturation point for proprioceptive recalibration. That is, the amount of proprioceptive recalibration is constrained such that the estimate of hand position is not too different from the actual hand position. Similar constraints have been proposed for other forms of cross-sensory calibration (Zaidel, Ma, and Angelaki 2013; Zaidel, Turner, and

Angelaki 2011). Given this "quota" for proprioceptive recalibration, there may be a trade-off between the amount of PS_{vis} and PS_{drift}: A larger PS_{vis} in Exp 1 leaves less room for PS_{drift}, and a lower PS_{vis} in Exp 2, in turn, leaves more room for PS_{drift}.

We recognize that the arguments presented here rest on a number of untested assumptions. We offer these speculations to highlight issues in our results that remain puzzling and will require future experiments to fully unravel.

Addressing concerns with correlational analyses

We recognize that our two main results are correlational: 1) The positive correlation between proprioceptive variability and the upper bound of adaptation and 2) the negative correlation between proprioceptive shift and the upper bound of adaptation. As with any correlational analysis, we must be cautious about inferring causation and also recognize that there may be hidden variables mediating the correlations. An example of the latter might be the effect of motivation/attention and how variation on these dimensions might impact *both* proprioception (shift/variability) and motor behavior (upper bound of adaptation). A difference between motivated and unmotivated participants could drive both effects. For instance, a "bad" subject may simultaneously exhibit greater proprioceptive shift (being more susceptible to the visual cursor feedback, despite instructions to ignore it) as well as a larger upper bound (e.g., failing to ignore the clamped feedback as instructed in Experiment 2 and aiming away from the target to try and negate the perturbation).

One way to address this is to consider other comparisons where a correlation would be expected based on individual differences in motivation/attention. In our study, the measures we expect would be most sensitive to motivation/attention would be:

1) Reach variability, defined as the standard deviation of the detrended hand angle data across the entire experiment.

2) Reaction time variability, defined as the standard deviation of the detrended RT data across the entire experiment.

3) The time taken to make a proprioceptive judgement during proprioceptive probe trials.

The above is based on the assumption that "bad" subjects would display noisier and more erratic reaches, leading to greater variability in hand angle and greater variability in RT. We might also assume that "bad" subjects would be sluggish in making their proprioceptive judgements, manifest as longer proprioceptive probe times.

We correlated these "control" measures for motivation/attention with our core measures of proprioceptive shift, proprioceptive variability, and the upper bound of adaptation. As a conservative measure, we did not perform any family-wise correction on the p values. With one exception, none of the correlations between these "control" measures and our measures of proprioception and the upper bound of adaptation were significant (Table 2.4). The exception was the positive correlation between proprioceptive variability and reaching variability, but this only held in Exp 2. Moreover, reach variability correlated only with proprioceptive variability and not with the upper bound of adaptation. In sum, these analyses suggest that individual differences in motivation/attention are unlikely to provide a third variable account of the main correlations predicted by our models and observed empirically.

Table 2.4

Control Variable	Dependent Variable	Exp 1		Exp 2	
		R	P	R	P
Reach variability	Prop shift	0.24	0.19	-0.17	0.40
	Prop var	0.14	0.40	0.38	0.03
	Aftereffects or asymptote	0.07	0.71	0.29	0.10
RT variability	Prop shift	0.09	0.64	-0.06	0.70
	Prop var	0.28	0.10	0.15	0.40
	Aftereffects or asymptote	-0.22	0.24	0.25	0.20
Proprioceptive probe time	Prop shift	0.25	0.20	-0.05	0.80
	Prop var	-0.21	0.30	0.22	0.20
	Aftereffects or asymptote	-0.26	0.20	0.04	0.80

Experimental Variable	Dependent Variable	Exp 1		Exp 2	
		R	P	R	P
Prop shift	Aftereffects or asymptote	-0.40	0.03	-0.62	<0.01
Prop var		0.49	<0.01	0.39	0.03

Chapter 3: Understanding implicit sensorimotor adaptation as a process of proprioceptive re-alignment

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The empirical results from the previous chapters led us to develop a new, kinesthetic re-alignment model of implicit adaptation. I will formalize this model in this chapter, demonstrating how it readily explains the non-monotonic time course of perceived hand position during implicit adaptation (Chapter 1 and the relationship between kinesthetic biases/uncertainty with the extent of implicit adaptation (Chapter 2). Moreover, I will demonstrate how the kinesthetic re-alignment model is consistent with many phenomena that have previously been interpreted in terms of learning from visual errors, and offers a parsimonious account of numerous unexplained phenomena.

Implicit adaptation of the sensorimotor system

Motor adaptation is an essential feature of human competence, allowing us to flexibly move in novel and dynamic environments (Kim, Avraham, and Ivry 2020; Krakauer et al. 2019; Ryan Morehead and de Xivry 2021; Shadmehr, Smith, and Krakauer 2010). A sailor adjusts her sails in response to variations in the wind; a basketball player fights against fatigue to maintain a similar force output. Motor adaptation refers to the processes that ensure well-learned movements remain accurate across a broad range of contexts.

Motor adaptation is not a unitary operation but relies on multiple learning processes. Paralleling the memory literature, one broad distinction can be made between processes that are under conscious control and those that operate outside awareness. To continue with the sailing example, a skilled skipper can strategically adjust the sails to achieve a desired heading, while implicitly maintaining that heading based on subtle fluctuations in the rope's tension. The interplay of explicit and implicit processes in sensorimotor adaptation has been the focus of many studies over the past decade. Whereas the former is volitional and well-suited for rapid modifications in behavior, the latter occurs automatically and operates over a slower time scale (Huberdeau, Krakauer, and Haith 2019; Hegele and Heuer 2010; McDougle, Ivry, and Taylor 2016; Werner et al. 2015).

Computationally, explicit and implicit processes for adaptation are constrained to solve different problems: Whereas explicit processes focus on goal attainment, implicit processes are designed to ensure that the selected movement is flawlessly executed (Taylor and Ivry 2011). Consistent with this distinction, the deployment of aiming strategies to offset an experimentally imposed perturbation requires prefrontal control (Anguera et al. 2010; Benson, Anguera, and Seidler 2011; Taylor and Ivry 2014), whereas implicit adaptation is dependent on the integrity of the cerebellum (Butcher et al. 2017; Haar and Donchin 2020; Hadjiosif et al. 2014; Izawa, Criscimagna-Hemminger, and Shadmehr 2012; Schlerf et al. 2013; Taylor, Klemfuss, and Ivry 2010; Tseng et al. 2007; Tzvi, Loens, and Donchin 2021).

One paradigmatic way to study motor adaptation is to introduce a visuomotor perturbation between the motion of the arm and the corresponding visual feedback. Historically, such visuomotor perturbations were accomplished with prism glasses that introduced a translation in the visual field (Helmholtz 1924; Kitazawa, Kohno, and Uka 1995; Petitet, O'Reilly, and O'Shea 2018; G. M. Redding and Wallace 2001). Nowadays, motion tracking and digital displays enable more flexible control over the relationship between hand position and a feedback signal (Krakauer et al. 2000; Krakauer, Ghez, and Ghilardi 2005). In a typical study, participants are instructed to make reaching movements towards a visual target on a horizontally mounted computer monitor (Figure 3.1A). By positioning the hand below the display, vision of the hand is occluded. However, a visual cursor is presented on the monitor to indicate hand position, a signal that is readily incorporated into the body schema if its spatial and temporal properties are correlated with the movement. After a few reaches to familiarize the participant with the task environment, a rotation (e.g., 45°) is introduced between the motion of the hand and the visual cursor. If participants continued to move directly to the target, the cursor would miss the target, introducing a visual error. Over several reaches, participants adapt to this perturbation, with the hand's heading angle shifted in the opposite direction of the rotation.

The aggregate behavioral change in response to a large perturbation is driven by a combination of strategic aiming and implicit adaptation. One source of evidence originates from a study examining how people respond to visuomotor rotations of varying sizes (Bond and Taylor 2015). Explicit strategy use, as measured by verbal aim reports, was dominant when the error size was large, producing corrective adjustments in reaching direction that scaled with the size of the rotation (Figure 3.1B, adapted from Figure 7A in Bond and Taylor, 2015). Yet, the extent of implicit adaptation, as measured by no-feedback aftereffects trials in which participants were instructed to "move directly to the target" without re-aiming, remained constant for perturbations ranging from 15° to 90°. Thus, while explicit re-aiming can flexibly compensate for errors of varying sizes, implicit adaptation saturates, at least for large errors.

The rigidity of implicit adaptation is evident in a variety of other methods (Hegele and Heuer 2010; Maresch, Werner, and Donchin 2020; Mazzoni and Krakauer 2006; Taylor, Krakauer, and Ivry 2014; Werner et al. 2015). The "visual clamped feedback" task provides an especially striking method to study implicit adaptation without contamination from explicit processes (R. Morehead et al. 2017). With clamped feedback, the angular trajectory of the cursor is invariant with respect to the target, always following a trajectory that is offset from the target by a fixed angle. As such, the direction in which the cursor moves is not contingent on the direction of the participant's movement. Participants are instructed to always reach directly to the target and ignore the visual cursor. Despite being fully aware of the manipulation, participants adapt, with the heading angle shifting in the opposite direction of the rotation in an automatic and implicit manner. Although the size of the visual error never changes, adaptation eventually reaches an upper bound, averaging between 15° - 25° away from the target. Consistent with the results of Bond and Taylor (Bond and Taylor 2015), this asymptote does not vary across a wide range of clamped rotation sizes (Kim et al. 2018; Neville and Cressman 2018; Jonathan S. Tsay, Lee, et al. 2021; Jonathan S. Tsay, Irving, and Ivry 2022).

The visuo-centric view of implicit sensorimotor adaptation

Implicit adaptation in response to visuomotor perturbations has been framed as an iterative process, designed to minimize a *visual* error (Cheng and Sabes 2006; Donchin, Francis, and Shadmehr 2003; Herzfeld et al. 2014; Kim et al. 2018; Mazzoni and Krakauer 2006; R. Morehead et al. 2017; Thoroughman and Shadmehr 2000; D. M. Wolpert, Miall, and Kawato 1998). The visual error experienced on the previous trial is used to modify the visuomotor map, such that the motor command on a subsequent trial will be adjusted to reduce that error. According to this visuo-centric view, the extent of implicit adaptation represents a point of equilibrium, one at which the trial-by-trial change in heading angle in response to the visual error is counterbalanced by the trial-by-trial decay ("forgetting") of this modified visuomotor map back to its baseline, default state (R. Morehead and Smith 2017) (Figure 3.1C).

A widely employed model of implicit adaptation posits that trial-to-trial learning is driven by a visual error (e):

3.1 $$x_{t+1} = Ax_t + Ke_t$$

The learning process is controlled by a learning rate (K), which specifies how much is learned from the visual error. The forgetting process is controlled by a retention parameter (A). These two processes dictate how the participant's state (x) (e.g., hand trajectory) changes over time, from trial t to trial t + 1. The upper bound of implicit adaptation (x_{UB}) is achieved when x_{t+1} is equal to x_t. Rearranging these terms shows that the upper bound is achieved when the amount of forgetting ($1 - A$) is equal to the amount of learning induced by the visual error (Eq 3.2):

3.2 $$(1 - A)x_{UB} = Ke_t$$

By further re-arranging these terms, one can appreciate that the rate and asymptote of implicit adaptation (x_{UB}) are determined by two fixed parameters, the learning and forgetting rates (Eq 2.3). By this view, the change in the sensorimotor map following a given trial will be a fixed proportion of the visual error size. That is, the rate will scale with error size. Similarly, the asymptote would also scale, reaching a final level at which the change resulting from the response to the visual error on the previous trial is in equilibrium with the amount of forgetting on the previous trial.

3.3 $$x_{UB} = \frac{Ke_t}{(1 - A)}$$

Variants of this visuo-centric model have been introduced over the years to account for a wide range of observations. For example, several studies have observed that the rate and extent of adaptation saturates for large visual errors (Marko et al. 2012; Wei and Körding 2009; Kim et al. 2018; R. Morehead et al. 2017). To accommodate this effect, some models center on the notion that the motor system reduces its learning rate (K) in response to large visual errors, an argument that is motivated by the idea that large errors are rare, and likely due to external events rather than error within the motor system (Shams and Beierholm 2010; Wei and Körding 2009; Herzfeld et al. 2014). Another hypothesis is that short-term plasticity is limited within the motor system, with the upper bound reflecting the maximum amount of behavioral change the motor system can accommodate (Kim et al. 2018). While these models differ in how they are implemented, they all suggest that implicit adaptation is driven by a visual error, and that an asymptote is reached at the equilibrium between learning and forgetting.

This visuo-centric perspective on adaptation is appealing. Not only does it fit with a zeitgeist which holds vision as a "dominant" sense, but it also matches our intuition of how we view task success: In day-to-day life, we frequently interact with visual objects, whether it be picking up a glass of water or moving the computer mouse over a desired icon. When a perturbation is introduced, we try to re-establish conditions such that the visual feedback is once again reinforcing. In visuomotor adaptation studies, the experimenter manipulates where the cursor is presented (Krakauer et al. 2000) or when the visual cursor is shown (Brudner et al. 2016; Honda, Hirashima, and Nozaki 2012;

Kitazawa, Kohno, and Uka 1995; Wang et al. 2021). The resultant change in hand trajectory is interpreted as a response to nullify the visual error. A dramatic demonstration of visual dominance comes from the study of deafferented monkeys and humans who have lost their sense of proprioception and haptics. Despite their sensory loss, deafferent individuals adapt in a similar manner as those observed in control participants (Bernier et al. 2006; Sarlegna et al. 2010), indicating that vision alone is sufficient to drive implicit adaptation (Blouin et al. 1993; Fleury et al. 1995; Lefumat et al. 2016; Sarlegna et al. 2010; Yousif et al. 2015; Taub and Goldberg 1974).

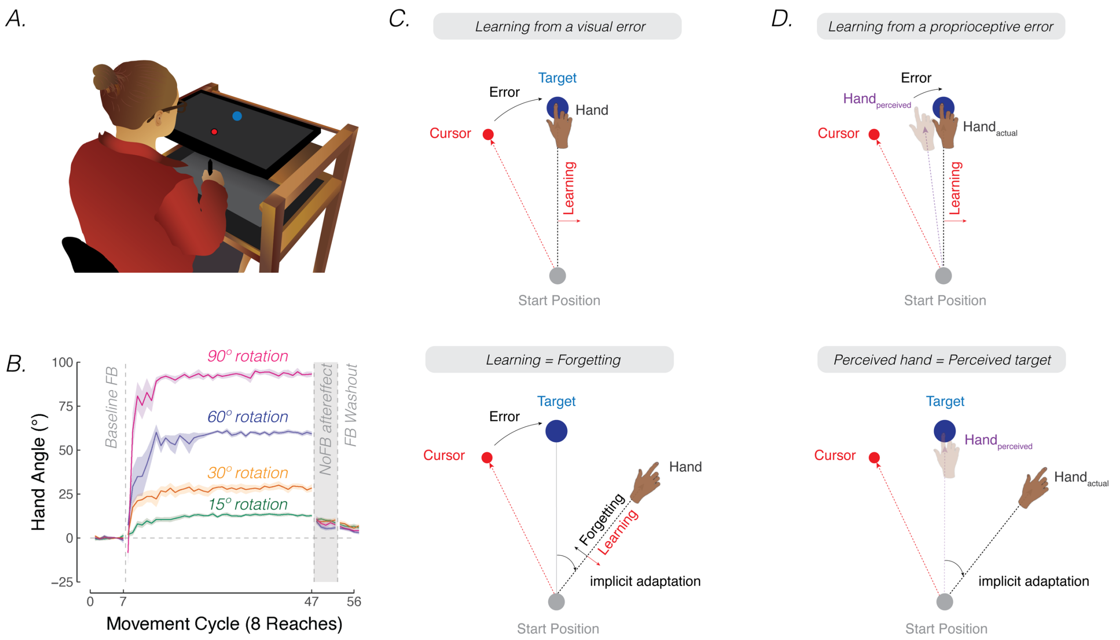

Figure 3.1. Contrasting visuo-centric and proprioceptive-centric views of implicit motor adaptation. **A)** Experiment setup. **B)** Mean time courses of hand angle for 15° (green), 30° (yellow), 60° (purple), and 90° (pink) rotation conditions (adapted from Figure 7A in Bond and Taylor, 2015). Hand angle is presented relative to the target (0°) during veridical feedback, rotation, and no-feedback trials (grey background). Hand angle is similar during the no-feedback trials for all four perturbation sizes, indicating equivalent implicit adaptation. Shaded region denotes SEM. Note that Bond and Taylor (2015) used eight target locations, and thus, had eight reaches per cycle. **C)** The cursor feedback (red dot) follows a trajectory that is rotated relative to the line connecting the start position and target (blue dot). With visual clamped feedback, the angular trajectory of the visual cursor is not spatially tied to the angular trajectory of the participant's (hidden) hand but follows a trajectory that is at an invariant angle relative to the target. Despite awareness of the manipulation and instructions to always reach directly to the target, participants show a gradual change in heading direction that eventually reaches an asymptote. According to visuo-centric models, the goal of implicit adaptation is to minimize a visual error (i.e., error = visual cursor – target; upper panel), with the extent of implicit adaptation being the point of equilibrium between learning and forgetting (lower panel). **D)** According to the proprioceptive re-alignment model (PReMo), the goal of implicit adaptation is to minimize a proprioceptive error (i.e., error = perceived hand position – target, upper panel). The perceived (shaded) hand position is influenced by the actual, the expected (based on efference copy), and seen (i.e., visual cursor) hand location. The extent of implicit adaptation corresponds to the point in which the perceived hand position is at the target (lower panel).

The neglected role of proprioception

Despite its appeal, the visuo-centric view is an oversimplification. The brain exploits all of our senses: While olfaction may not be essential for precisely controlling the limb, proprioception, the perception of body position and body movement, is certainly critical for motor control (Sober and Sabes 2003, 2005). The classic work of Mott and Sherrington at the end of the 19th Century demonstrated that surgical deafferentation of an upper limb produced severe disorders of movement in the monkey (Mott and Sherrington 1895). The actions of the animal indicated that the intent was intact, but the movements themselves were clumsy, inaccurate, and poorly coordinated (Bossom 1974; Munk 1909). Humans who suffer neurological disorders resulting in deafferentation show a surprising capability to produce well-practiced movements, yet these individuals have marked deficits in feedback control (Rothwell et al. 1982; Sanes et al. 1985). Indeed, recent work indicates that healthy participants rely almost exclusively on proprioceptive information for rapid feedback control, even when visual information about the limb is available (Crevecoeur, Munoz, and Scott 2016).

A large body of work underscores the important role of proprioception in sensorimotor adaptation. First, deafferented individuals fail to generate specific patterns of isometric and isotonic muscle contractions in a feedforward manner as they initiate rapid elbow flexion (Forget and Lamarre 1987; Gordon, Ghilardi, and Ghez 1995). Second, neurologically healthy and congenitally blind individuals can adapt to a force-field perturbation without the aid of vision, presumably relying solely on proprioceptive input (DiZio and Lackner 2000; Striemer, Enns, and Whitwell 2019; Franklin et al. 2007; Marko et al. 2012). Third, when opposing visual and proprioceptive errors are provided, aftereffects measured during the no-feedback block after adaptation are in the direction counteracting the proprioceptive error instead of the visual error. Although it is possible that strategic effects extended into the aftereffect block, this result would suggest that proprioceptive errors can be prioritized over visual errors (Hayashi, Kato, and Nozaki 2020) (also see: (Haswell et al. 2009)). Fourth, honing in on tasks that have eliminated strategy use, individual differences in proprioception are robustly correlated with the extent of *implicit* adaptation (Jonathan S. Tsay, Kim, Parvin, et al. 2021; Salomonczyk, Cressman, and Henriques 2013; Ruttle, Hart, and Henriques 2021) (but see: (Vandevoorde and Orban de Xivry 2021)). That is, both proprioceptive uncertainty during baseline and proprioceptive biases induced by a visuo-proprioceptive discrepancy are associated with greater aftereffects (Feature 1 and 3).

Despite these observations, the computational role of proprioception in implicit motor adaptation is unclear. In some models, proprioception is seen as playing a passive role, a signal that is biased by vision but does not drive implicit adaptation (Mattar, Darainy, and Ostry 2013; Ohashi, Gribble, and Ostry 2019; Ohashi et al. 2019). Other models consider a contribution of proprioception to implicit adaptation, but the computational principles of how this information is used have not been elucidated (Rossi, Bastian, and Therrien 2021; Ruttle, Hart, and Henriques 2021; Salomonczyk, Cressman, and Henriques 2013; Zbib, Henriques, and Cressman 2016).

In this review article, we present a new model of sensorimotor adaptation, the proprioceptive re-alignment model (PReMo). The central premise of the model is that proprioceptive error is the primary driver of implicit adaptation, solving the computational problem of ensuring an alignment of the perceived and desired position of the hand. After laying out a set of core principles motivating the model, we present a review of the adaptation literature through this new lens to offer a parsimonious and novel account of a wide range of phenomena. Given that much of the evidence reviewed here is based on correlational studies, we conclude by outlining directions for future experimental manipulations that should provide strong tests of PReMo.

Interaction of Visual and Proprioceptive Information

Perception depends on a combination of multisensory inputs, contextualized by our expectations (Rock 1983). In reaching to pick up objects in the environment, the location of the hand is specified by afferent inputs from muscle spindles that convey information about muscle length/velocity as well as by visual information relayed by photoreceptors in the eye (Proske and Gandevia 2012). Estimates of hand position from these signals, however, may not be in alignment due to noise in our sensory systems or perturbations in the environment. To resolve such disparities, the brain shifts the perception of discrepant representations towards one another – a phenomenon known as sensory recalibration.

In the case of a visuomotor rotation, exposure to the systematic discrepancy between vision and proprioception results in a reciprocal interaction between the two sensory signals. As shown in many studies, there is a pronounced shift in the perceived hand position towards the visual cursor, an effect that is referred to as a proprioceptive shift (Burge, Girshick, and Banks 2010; Cressman and Henriques 2010; Recanzone 1998; Synofzik, Lindner, and Thier 2008; Synofzik, Thier, and Lindner 2006; K. van der Kooij et al. 2013; Katinka van der Kooij, Overvliet, and Smeets 2016). There is also a shift in the perceived location of the cursor towards the hand (i.e., visual shift) (M. Rand and Heuer 2019a; Simani, McGuire, and Sabes 2007; H. J. Block and Bastian 2011) (see Appendix, "The contribution of visual shifts in PReMo"). For large discrepancies between vision and proprioception, this recalibration process does not result in a unified percept. Rather the shift within each modality saturates as the visuo-proprioceptive discrepancy increases. For example, visuomotor rotations of either 15° or 30° will result in a 5° shift in proprioception towards the visual cursor and a 1° shift in vision towards the actual hand position (Salomonczyk, Cressman, and Henriques 2013; M. Rand and Heuer 2019a; H. J. Block and Bastian 2011). [Footnote 3.1: One critical difference between sensory recalibration and sensory integration is in terms of the resulting percept. As commonly conceptualized (but see Footnote 3.2), sensory integration results is a unified percept of hand position by combining sensory information in a weighted fashion based on their relative uncertainties (Burge, Ernst, and Banks 2008; Van Beers, Sittig, and Gon 1999). It is a transient phenomenon that is measured only when *both* modalities are present. In contrast, sensory recalibration is an enduring bias that can be observed when each sensory modality is assessed independently.]

Sensory expectations also play a role in sensory recalibration ('t Hart and Henriques 2016). For instance, perception of the moving limb is biased towards the direction of the motor command (e.g., a visual target) (Bhanpuri, Okamura, and Bastian 2013; Blakemore, Wolpert, and Frith 1998; Gaffin-Cahn, Hudson, and Landy 2019; Gandevia and McCloskey 1978; Kilteni, Engeler, and Ehrsson 2020; Lanillos, Franklin, and Franklin 2020; McCloskey, Ebeling, and Goodwin 1974). One model suggests that the cerebellum receives an efference copy of the descending motor command and generates a prediction of the expected sensory consequences of the movement. This prediction is widely relayed to different regions of the brain, providing a form of predictive control (Grüsser 1994; Sperry 1950; von Holst and Mittelstaedt 1950; D. M. Wolpert and Miall 1996). In sum, sensory recalibration seeks to form a unified percept of hand position by combining sensory inputs and sensory expectations (Körding and Wolpert 2004).

Sensory recalibration has several notable features: First, sensory recalibration effects are enduring and can be observed even when each sensory modality is assessed alone. For instance, after exposure to a visual perturbation, a visual shift is observed when participants are asked to judge the position of a briefly flashed visual cursor (Simani, McGuire, and Sabes 2007). Similarly, a proprioceptive shift is observed when participants locate their unseen hand using a touch screen (Ruttle, Hart, and Henriques 2021). Second, these shifts occur rapidly (Ruttle et al. 2016; Ruttle, Hart, and Henriques 2021; Ruttle, 't Hart, and Henriques 2018), with both the visual and proprioceptive shift reaching asymptotic values within just a few reaches after the introduction of a visuomotor perturbation (Ruttle et al. 2016). In the following section, we formalize how sensory recalibration during visuomotor adaptation drives implicit adaptation. Third, as noted above, while the extent of recalibration is a fixed ratio for small visuo-proprioceptive discrepancies (Zaidel, Turner, and Angelaki 2011), the magnitude of the change within each modality exhibits marked saturation (Salomonczyk, Cressman, and Henriques 2013; Jonathan Sanching Tsay, Parvin, and Ivry 2020; Jonathan S. Tsay, Kim, Parvin, et al. 2021).

The proprioceptive re-alignment model (PReMo)

Reaching movements are enacted to transport the hand to an intended goal. In most situations, that goal is to pick up an object such as the fork at the dinner table. The resultant feedback allows the brain to evaluate whether the movement ought to be modified. This feedback can come from vision, seeing the hand miss the fork, as well as proprioception, gauging the position of the hand as it misses the fork. The sensorimotor system exploits these multiple cues to build a unified percept of the position of the hand. When the action falls short of meeting the goal – the fork is missed or improperly grasped – adaptation uses an error signal to recalibrate the system. In contrast to visuo-centric models, we propose that the fundamental error signal driving adaptation is proprioceptive, the mismatch between the perceived and desired hand position (Figure 3.1D, top). From this perspective, the upper bound of implicit adaptation will correspond to the point at which the hand is perceived to be aligned with the target. In this section, we formally develop this proprioceptive re-alignment model (PReMo).

Perceived hand position is determined by sensory recalibration

As noted above, perceived hand position is determined by a multitude of sensory inputs and sensory expectations. Prior to the crossmodal interaction between vision and proprioception, we assume that the system generates an optimal *intramodal* estimate of hand position using the weighted average of the actual position of the hand ($x_{p,t}$) and the expected position of the hand based on an outgoing motor command (Figure 3.2A-B). This motor command is selected to achieve a proprioceptive goal, G_t. Therefore, the proprioceptive *integrated hand position* ($x^I_{p,t}$) is given by: [Footnote 3.2: As noted in Footnote 3.1, the term “integration” is sometimes used to refer to the combination of information from two different sensory modalities (e.g., the *crossmodal* combination of the observed cursor and felt hand position). In this review, we will reserve the term “integration” in an intramodal sense, referring to the combination of the input from a sensory modality and the expected position of that sense based on the outgoing motor command (e.g., for proprioception, the actual and expected hand position; for vision, the actual and expected cursor position). We also note that the proprioceptive movement goal is typically assumed to be the visual target. However, if participants were to use an aiming strategy to compensate for a perturbation, the movement goal would then correspond to the aiming location].

$$x^I_{p,t} = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_p^2} x_{p,t} + \frac{\sigma_p^2}{\sigma_u^2 + \sigma_p^2} G_t \tag{3.4}$$

σ_u^2 represents the uncertainty of sensory expectations/predictions given a motor command to the goal, which may be influenced by both extrinsic sources of variability (e.g., greater perturbation variability in the environment) and intrinsic sources of variability (e.g., greater motor noise). σ_p^2 represents uncertainty in the proprioceptive system.

Correspondingly, the optimal *intramodal* integrated estimate of the visual cursor position ($x^I_{v,t}$) is the weighted average of the actual position of the cursor ($x_{v,t}$) and the expected position of the cursor based on outgoing motor commands (G_t):

3.5 $$x^I_{v,t} = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_v^2} x_{v,t} + \frac{\sigma_v^2}{\sigma_u^2 + \sigma_v^2} G_t$$

where σ_v^2 represents uncertainty in the visual system. This intramodal integrated estimate of hand position is recalibrated crossmodally by vision (proprioceptive shift, β_p), resulting in a perceived hand position ($x^{per}_{p,t}$) (Figure 3.2C):

3.6 $$x^{per}_{p,t} = x^I_{p,t} + \beta_p$$

Correspondingly, the intramodal integrated estimate of cursor position is recalibrated crossmodally by proprioception (visual shifts, β_v), resulting in a perceived cursor position ($x^{per}_{v,t}$):

3.7 $$x^{per}_{v,t} = x^I_{v,t} + \beta_v$$

While the exact computational rules that govern the magnitude of crossmodal shifts (β_p, β_v) remain an active area of research (Hong, Badde, and Landy 2020), we assume that the perceptual shifts follow three general principles based on observations reported in the previous literature:

A. For small discrepancies, the degree of crossmodal recalibration is a fixed ratio (i.e., $\eta_{p,}\ \eta_v$) of the visuo-proprioceptive discrepancy (i.e., $x^I_{v,t} - x^I_{p,t}$). For larger discrepancies, the magnitude of the shift for each modality saturates (i.e., $\beta_{p,sat}$, $\beta_{v,sat}$) ('t Hart, Ruttle, and Henriques 2020; Ruttle, Hart, and Henriques 2021; Salomonczyk, Cressman, and Henriques 2013; Synofzik, Lindner, and Thier 2008).

3.8 $$\beta_{p,t} = \min\left(\left|\eta_p\left(x^I_{v,t} - x^I_{p,t}\right)\right|, \left|\beta_{p,sat}\right|\right)$$

3.9 $$\beta_{v,t} = \min\left(\left|\eta_v\left(x^I_{v,t} - x^I_{p,t}\right)\right|, \left|\beta_{v,sat}\right|\right)$$

Proprioceptive shifts and visual shifts towards the other modality are assigned negative values and shifts away from the other modality are assigned positive values (e.g., a 5° proprioceptive shift towards the cursor: $\beta_p = -5°$).

B. Visual and proprioceptive shifts are global (Simani, McGuire, and Sabes 2007; M. Rand and Heuer 2019b, 2020). This implies that the perceived hand position is not only shifted in the region of space near the biasing source (i.e., the target or feedback cursor), but will also be shifted in the same direction across the workspace (e.g., at the start position).

C. Crossmodal recalibration (proprioceptive shift and visual shift) decays in the absence of visual feedback (decay parameter: A) (Babu et al. 2021). This decay parameter modulates proprioceptive and visual shifts only when visual feedback is removed. As such, this decay parameter does not have an influence in determining the rate and extent of implicit adaptation, but instead modulates the rate in which aftereffects following adaptation decay to baseline.

3.10
$$\beta_{p,t+1} = A\beta_{p,t}$$

3.11
$$\beta_{v,t+1} = A\beta_{v,t}$$

Proprioceptive error signal drives implicit adaptation

As stated in the previous section, the motor system seeks to align the perceived hand position with the movement goal. A proprioceptive shift induced by a visuo-proprioceptive discrepancy will misalign the perceived hand position with the movement goal, resulting in a proprioceptive error:

3.12
$$Prop\ Error = G_t - x_{p,t}^{per}$$

The proprioceptive error is used to update the sensorimotor map such that a subsequent motor command will bring the hand position closer to being in alignment with the target: As with most state space models, this update process operates with a learning rate (K) when a perturbation is present:

3.13
$$x_{p,t+1} = x_{p,t} + K(G_t - x_{p,t}^{per})$$

A key assumption of PReMo is that the upper bound of adaptation (x_p^{UB}) is determined as the position of the hand at which the proprioceptive error is eliminated (Eq 3.12: $G_t - x_{p,t}^{per} = 0$; i.e., the perceived hand position = the perceived motor goal). By plugging in the terms from Eq 3.4 and 3.6 for $x_{p,t}^{per}$, and assuming that the movement goal is at the target (i.e., 0°), the upper bound of adaptation can be derived by solving for the position of the hand:

3.14
$$x_p^{UB} = -\beta_p(1 + \frac{\sigma_p^2}{\sigma_u^2})$$

This equation has several important implications for the upper bound of implicit adaptation. First, the upper bound of adaptation will increase with proprioceptive uncertainty (↑ σ_p^2) (Eq 3.14) and the size of the proprioceptive shift (↑ β_p) (Eq 3.14). Second, the upper bound of adaptation will be attenuated when there is an increase in the noise associated with sensory expectations of the motor command (↑ σ_u^2) (Eq 3.14) (see Supplemental section titled: *Proprioceptive shift does not correlate with proprioceptive variability*).

Third, assuming that the proprioceptive shift saturates ($\beta_{p,sat}$) for a wide range of visuo-proprioceptive discrepancies, the proprioceptive error will saturate (Eq 3.15). As such, trial-by-trial motor updates (U_{sat}, Eq 3.16) and the extent of implicit adaptation (x_p^{UB}, Eq 3.17) will also saturate:

3.15 $$PropError_{sat} = G_t - (x_{p,t}^{I} + \beta_{p,sat})$$

3.16 $$U_{sat} = K(G_t - x_{p,t}^{per})$$

3.17 $$x_{p,sat}^{UB} = -\beta_{p,sat}(1 + \frac{\sigma_p^2}{\sigma_u^2})$$

Finally, the perceived location of the hand will follow a unique time course. Early in adaptation, the perceived hand position is biased towards the visual cursor due to the proprioceptive shift (Figure 3.1D, top). This results in a proprioceptive error, the difference between perceived hand position and the visual target, the signal presumed to drive the heading angle of the movement away from the target (and cursor). Late in adaptation, the actual position of the hand will reach a point in which the perceived hand is felt at the target (Figure 3.1D, bottom); thus, the proprioceptive error is eliminated, and implicit adaptation ceases. This last conjecture encapsulates the essence of PReMo (see Feature 2, Figure 3.7B).

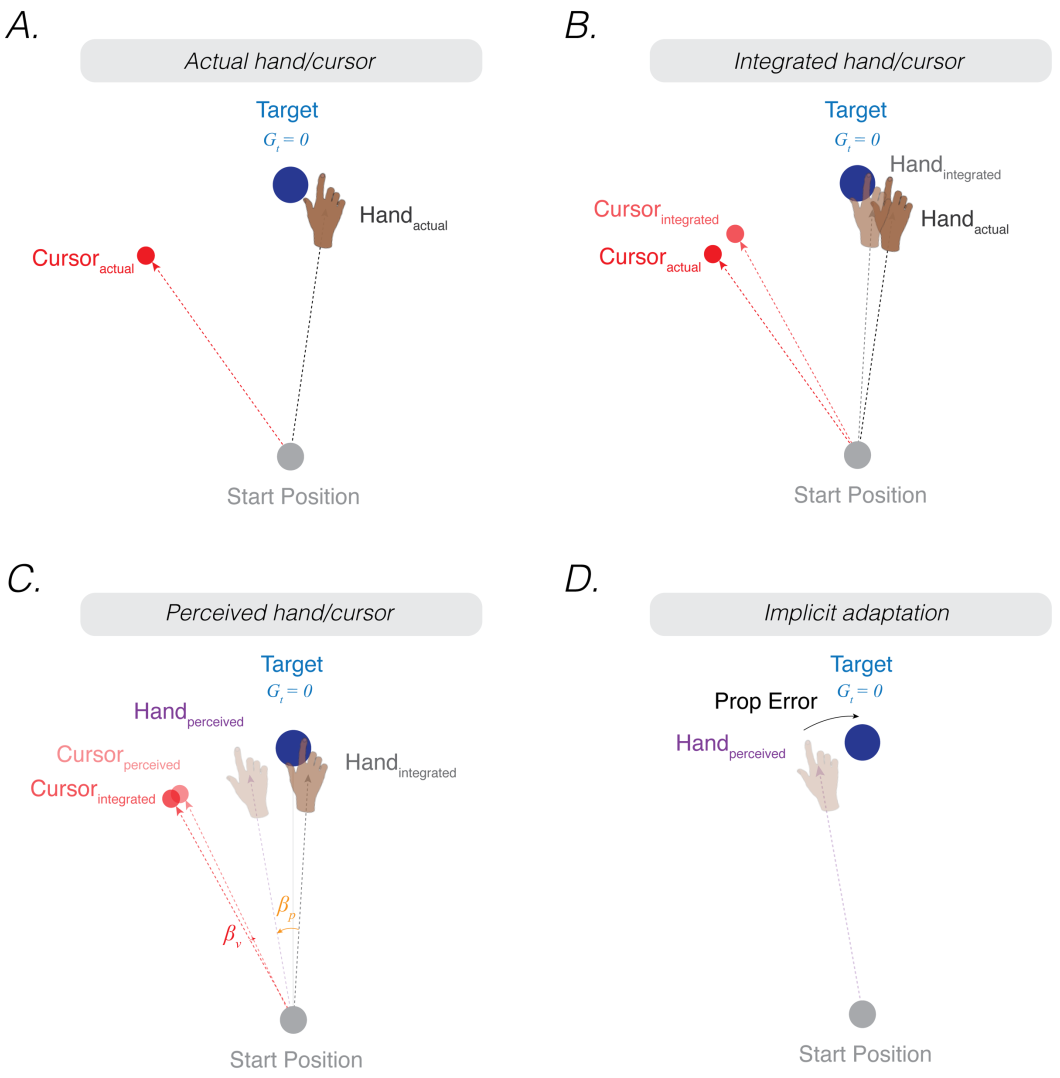

Figure 3.2. The proprioceptive re-alignment model (PReMo). **A)** When the feedback is rotated, the position of the feedback cursor (red dot) is rotated counterclockwise with respect to the location of the unseen hand (deviation depicted here arises from motor noise). **B)** Due to intramodal integration of sensory input and sensory expectations from the motor command, the integrated hand would lie between the visual target and the actual position of the hand, and the integrated cursor would lie between the visual target and the actual cursor. **C)** Due to crossmodal sensory recalibration, the integrated hand shifts towards the integrated cursor (proprioceptive shift, β_p) and the integrated cursor shifts towards the integrated hand (visual shift, β_v), forming the perceived hand and perceived cursor locations. **D)** The proprioceptive error (mismatch between the perceived hand position and the target, G_t) drives implicit adaptation in the clockwise direction, opposite to the imposed counterclockwise rotation.

Empirical support for the proprioceptive re-alignment model

In this section, we review key observations that have motivated the development of PReMo, focusing on studies that are relevant to core features of the model. We note at the outset that much of the evidence presented in this review is correlational in nature. Recognizing this limitation, we highlight predictions derived from PReMo to be tested in future experimental studies.

Feature 1. Implicit adaptation is correlated with proprioceptive shift

A core observation that spurred the development of PReMo is the intimate link between the proprioceptive shift and extent of implicit adaptation. One common method to quantify measures of proprioception involves asking participants to report the position of their hand after passive displacement (Figure 3.3A). The psychometric function derived from these reports is used to estimate the participants' bias and variability (see Feature 3 below for an extended discussion on proprioceptive variability). The proprioceptive judgements (i.e., "indicate where you feel your hand") are usually obtained before and after the visual feedback is perturbed, and as such, can be used to quantify the proprioceptive shift (i.e., change in proprioceptive bias, β_p; note that this measure is not the same as perceived hand position, x_p^{per}). Across a range of experiments, two notable characteristics stand out: 1) The proprioceptive shift saturates at ~5° and 2) reaches an asymptotic value after only a couple of trials of exposure to a visuo-proprioceptive discrepancy (H. J. Block and Bastian 2011; Cressman and Henriques 2010; Gastrock, Modchalingam, 't Hart, et al. 2020; Modchalingam et al. 2019; M. Rand and Heuer 2019a).

[Footnote 3.3: Proprioceptive recalibration may differ between experimental setups in which the hand movement and visual feedback are co-planar or occur in different planes (e.g., horizontal hand movement with visual feedback on a vertically aligned monitor). In the latter case the proprioceptive estimate requires an extra coordinate transformation. Nevertheless, PReMo can account for proprioceptive recalibration/shifts if provided with a representation of the actual hand position, predicted hand position, and visual feedback regarding hand position, with the orthogonal case requiring a coordinate transformation. There is considerable behavioral and neural evidence showing that we perform coordinate transformations with considerable flexibility (Miller et al. 2018). Indeed, this ability allows us to endow prosthetics and tools with "proprioception" (Kieliba et al. 2021), perceiving them as extensions of our own bodies.]

Across individuals, the magnitude of the proprioceptive shift can be correlated with the extent of adaptation, operationalized as the magnitude of the aftereffect obtained after exposure to a visuomotor rotation (Ruttle, Hart, and Henriques 2021; Jonathan S. Tsay, Kim, Parvin, et al. 2021) or as the asymptotic change in reaching angle following exposure to visual clamped feedback (Jonathan S. Tsay, Kim, Parvin, et al. 2021). As can be seen in Figure 3.3 (Panels E-G), the magnitude of the shift is negatively correlated with the upper bound of implicit adaptation. That is, the more proprioception shifts towards the cursor position, the greater the extent of implicit adaptation away from the perturbed cursor. A similar pattern has been observed in many other studies (Clayton, Cressman, and Henriques 2014; Gastrock, Modchalingam, 't Hart, et al. 2020; Modchalingam et al. 2019; Salomonczyk, Cressman, and Henriques 2013, 2011; Simani, McGuire, and Sabes 2007).

The correlation between proprioceptive shift and the upper bound of adaptation is in accord with PReMo (Eq 3.14). A greater shift in perceived hand location towards the perturbed visual feedback would create a greater misalignment between the perceived hand position and the desired hand position (i.e., the perceived location of the target). As such, one would expect that a larger deviation in hand angle would be required to offset this shift. With the focus on the visual error signal, visuo-centric models of implicit adaptation do not consider how the visual perturbation impacts the perceived hand location. Thus, these models do not predict, or rather are moot on the relationship between proprioceptive shift and the upper bound of adaptation.

In the following section, we will explore five unexplained phenomena of implicit adaptation that can be accounted for by observed features of the shift in proprioception.

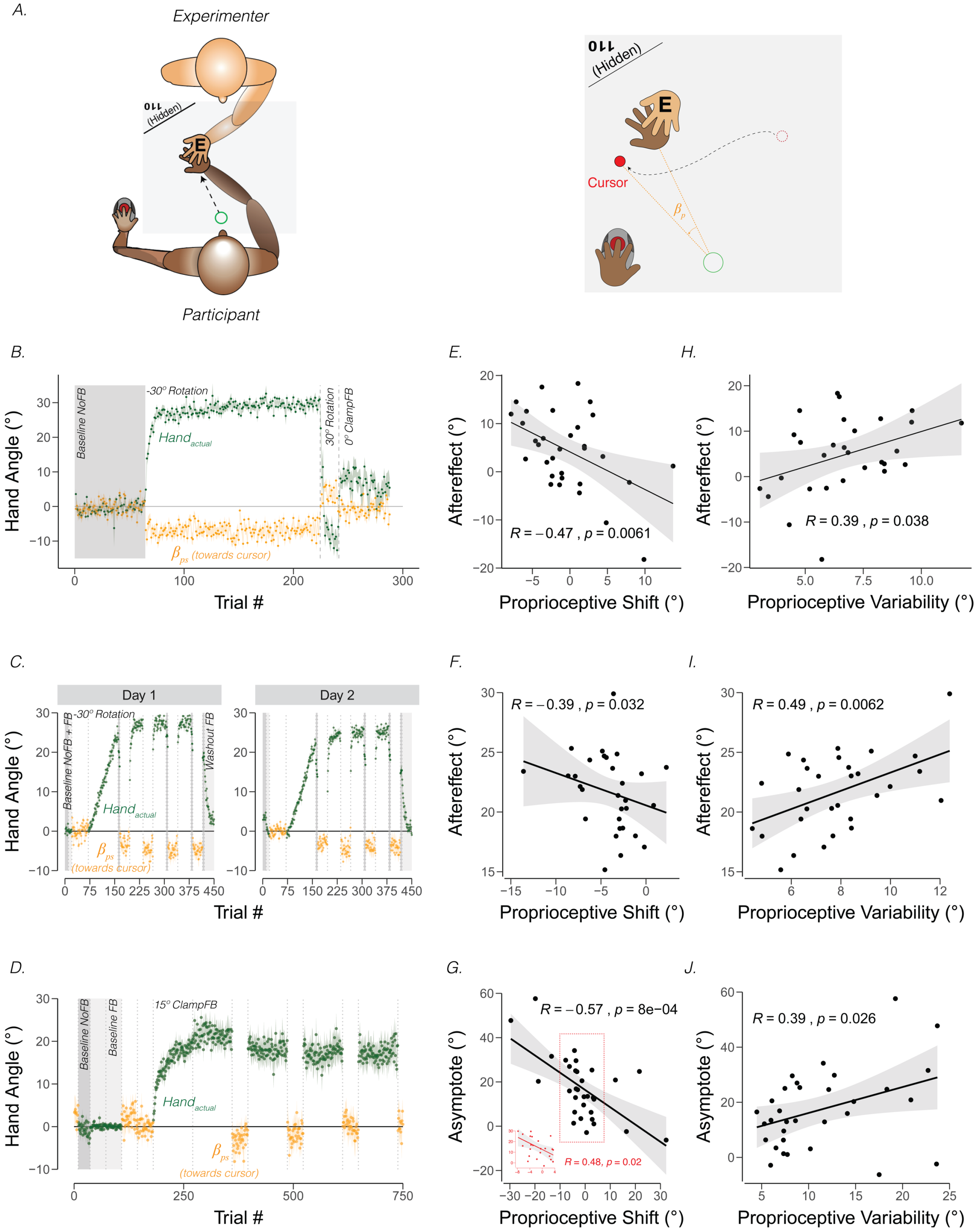

Figure 3.3. Proprioceptive shift and variability correlate with the upper bound of adaptation. **A)** Experimental setup for proprioceptive probe trials in Tsay et al (2021). The experimenter sat opposite the participant and moved the participant's hand from the start position to a location specified in the corner of the monitor (e.g., 110º) that was only visible to the experimenter. After the participant's hand was passively moved to the probe location, a cursor appeared at a random position on the screen (right panel). The participant used their left hand to move the cursor to the perceived hand position. A similar method was used in Ruttle et al 2021), but instead of the experimenter, a robot manipulandum was programmed to passively move the participant's arm. **B)** Abrupt visuomotor rotation design from Ruttle et al, 2021 (Exp 1; adapted from Figure 2a in Ruttle et al, 2021). After a baseline veridical feedback block, participants were exposed to a -30° rotated cursor feedback block, a 30° rotated feedback block, and a 0° clamped feedback block. Vertical dotted lines indicate block breaks. Green dots denote hand angle. Orange dots denote proprioceptive probe trials. Shaded error bars denote SEM. **C)** Gradual visuomotor rotation design from Tsay et al, 2021 (Exp 1; adapted from Figure 3a in Tsay et al, 2021). After baseline trials without feedback (dark grey) and veridical feedback (light grey), participants were exposed to a perturbation that gradually increased to -30º and then held constant. There were periodic proprioceptive probe blocks (orange dots) and no feedback motor aftereffect blocks (dark grey). **D)** Clamped rotation design from Tsay et al, 2021 (Exp 2; adapted from Figure 5a in Tsay et al, 2021). After a period of baseline trials, participants were exposed to clamped visual feedback that moves 15° away from the target. **E – G)** Correlation between proprioceptive shift and the extent of implicit adaptation. Note that the correlations are negative because a leftward shift in proprioception (towards the cursor) will push adaptation further to the right (away from the target and in the opposite direction of the cursor). Black dots represent individual participants. **H – J)** Correlation between variability on the proprioceptive probe trials during baseline and the extent of implicit adaptation in the three experiments depicted in B-D.

Feature 1, Corollary 1: The rate and extent of implicit adaptation saturates.

Many studies of sensorimotor adaptation have examined how the system responds to visual errors of varying size. Standard adaptation tasks that use a fixed perturbation and contingent visual feedback are problematic since behavioral changes that reduce the error also increase task success. To avoid this problem, two basic experimental tasks have been employed. First, the visual perturbation can vary in terms of both size and sign on a trial-by-trial basis, with the rate of implicit adaptation quantified as the change in hand trajectory occurring on trial n + 1 as a function of the visual error experienced on trial n (Hayashi, Kato, and Nozaki 2020; Wei and Körding 2009; Marko et al. 2012). By varying the sign as well as the size, the mean visual error is held around 0°, minimizing cumulative effects of learning. Second, clamped visual feedback can be used to look at an extended learning function to a constant visual error signal (Kim et al. 2018; R. Morehead et al. 2017). With these data, one can estimate an initial rate of implicit adaptation (e.g., change over the initial trials in response to a clamp), as well as measure the asymptotic value of adaptation. With traditional adaptation tasks, the asymptote of implicit adaptation can only be measured in an aftereffect block (Bond and Taylor 2015).

A striking result has emerged from this work, namely that the rate and extent of implicit adaptation is only proportional to the size of the error for small errors before saturating across a broad range of larger errors at around 5° (Figure 3.4) (Hayashi, Kato, and Nozaki 2020; Kasuga, Hirashima, and Nozaki 2013; Kim et al. 2018; Marko et al. 2012; R. Morehead et al. 2017; Jonathan S. Tsay, Lee, et al. 2021; Wei and Körding 2009; Jonathan S. Tsay, Najafi, Schuck, et al. 2022). As can be seen in Figure 3.4A, the rate (e.g., trial-to-trial change in hand angle) is relatively invariant in response to visual errors that exceed 10°. While variants of the standard visuo-centric model have been proposed to account for this saturation, none of them account for the association between proprioceptive shift and implicit adaptation.

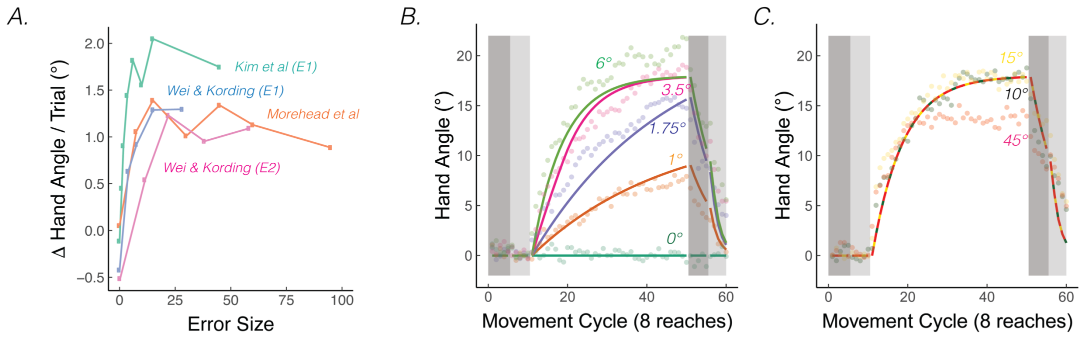

Figure 3.4. The rate of implicit adaptation saturate. **A)** Early adaptation rates saturate for studies using different methodologies. **B)** Data from Kim et al (2018). Different groups of participants made reaching movements with clamped visual feedback of varying sizes (0° - 45°; groups were divided into two panels for visualization purposes). Groups with smaller clamps (less than 6°) exhibited early adaptation rates that scaled with the size of the clamped feedback, but groups with larger clamped feedback (6° and above) showed a saturated early adaptation rate. Lines denote model fits of the proprioceptive re-alignment model ($R^2 = 0.953$).

PReMo offers a novel account of the saturation effect, one that shifts the focus from the motor system to the sensory system. As noted previously, the size of the proprioceptive shift saturates at a common value (~5°) across a wide range of visuo-proprioceptive discrepancies (Ruttle, Hart, and Henriques 2021; Salomonczyk, Cressman, and Henriques 2013; Synofzik, Lindner, and Thier 2008; Synofzik et al. 2010; Synofzik, Thier, and Lindner 2006; Jonathan Sanching Tsay, Parvin, and Ivry 2020; Mostafa et al. 2015). For example, the proprioceptive shift is essentially the same following the introduction of a 15° rotation or a 30° rotation (Jonathan S. Tsay, Kim, Parvin, et al. 2021). Since the size of the proprioceptive shift dictates the size of the proprioceptive error, we should expect an invariant rate and extent of motor adaptation in response to visual errors of different sizes (Eq 3.15-3.17). Even under experimental manipulations for which the proprioceptive shift scales with the size of small visual errors, the same scaling is mirrored in the extent of implicit adaptation ('t Hart, Ruttle, and Henriques 2020), further supporting the link between the proprioceptive shift and implicit adaptation.

Feature 1, Corollary 2: Proprioceptive shift at the start position explain patterns of generalization

Generalization provides a window into the representational changes that occur during sensorimotor adaptation. In visuomotor rotation tasks, generalization is assessed by exposing participants to the perturbation during movements to a limited region of the workspace and then examining changes in movements made to other regions of the workspace (Z. Ghahramani, Wolpert, and Jordan 1996; Pine et al. 1996). A core finding is that generalization of implicit adaption is local, with changes in trajectory limited to targets located near the training region (Krakauer et al. 2000; Tanaka, Sejnowski, and Krakauer 2009). These observations have led to models in which generalization is determined by the properties of directionally-tuned motor units, with the extent of generalization dictated by the width of their tuning functions (Tanaka, Sejnowski, and Krakauer 2009). As such, the error signal that drives implicit adaptation only produces local changes around the location where the error was experienced. From the lens of PReMo, this view of local generalization specifies how implicit adaptation attributable to proprioceptive re-alignment at the training target should affect movements to nearby target locations.

More intriguing, many studies have also found small, but reliable changes in heading direction to targets that are far from the training location, including at the polar opposite direction of training (Krakauer et al. 2000; Taylor, Hieber, and Ivry 2013; Pine et al. 1996; R. Morehead et al. 2017; Poh et al. 2021). For example, following an exposure phase in which a 45° CCW rotation was imposed on the visual feedback for movements to one target location, a 5° shift in the CW direction was observed for movements to probe locations more than 135° away (Figure 3.5C, Taylor et al (2013)). These far generalization effects have been hypothesized to reflect some sort of global component of learning, one that might be associated with explicit re-aiming (McDougle and Taylor 2019; Hegele and Heuer 2010; McDougle, Bond, and Taylor 2017). [Footnote 3.4: Unlike visuomotor adaptation, force-field adaptation does not appear to produce far generalization (Rezazadeh and Berniker 2019; Howard and Franklin 2015). Future research can evaluate how constraints on PReMo vary between different tasks. See Feature 6 about how PReMo generalizes from visuomotor rotation to force-field adaptation]

However, PReMo suggests an alternative interpretation, positing that far generalization arises as a consequence of the cross-sensory recalibration that comes about from exposure to the perturbation. Cross-sensory recalibration has been shown to result in visual and proprioceptive shifts that extend across the training space. That is, when proprioceptive judgements are obtained pre- and post-training, the resulting distortions of vision and proprioception are remarkably similar at the trained and probed locations around the workspace (Cressman and Henriques 2010; 't Hart, Ruttle, and Henriques 2020; Simani, McGuire, and Sabes 2007; 't Hart and Henriques 2016). Specifically, Simani et al. (2007) observed a robust proprioceptive shift at a generalization target 45° from the training location; this finding was extended in studies from the Henriques' group, revealing a robust proprioceptive shift as far as 100° from the training target ('t Hart and Henriques 2016; 't Hart, Ruttle, and Henriques 2020; Mostafa et al. 2015).

Assuming that the proprioceptive shift induced by a visuomotor rotation also affects the perceived hand location at the start position (an assumption yet to be directly tested), all movement trajectories planned from the perceived (shifted) hand position at the start position to a visual target located at any position within the workspace will be impacted (Sober and Sabes 2003; Vindras et al. 1998) (Figure 3.5A). This will yield a pattern of generalization that extends to far probe locations (Figure 3.5B). Specifically, the planned vector (solid red line; Figure 3.5A) would result in an actual clockwise movement with respect to the upward trained target (dotted blue line; Figure 3.5B) but a counterclockwise movement with respect to the bottom generalization targets. PReMo therefore provides a qualitative account of generalization as a combination of 1) a local pattern of generalization of implicit adaptation around the training target caused indirectly by the proprioceptive shift at the target location, and 2) a global pattern of generalization attributable to the proprioceptive shift at the start location. Future experiments should be conducted to quantify the relative contribution of these two components to the global pattern of generalization following adaptation to a visuomotor rotation.

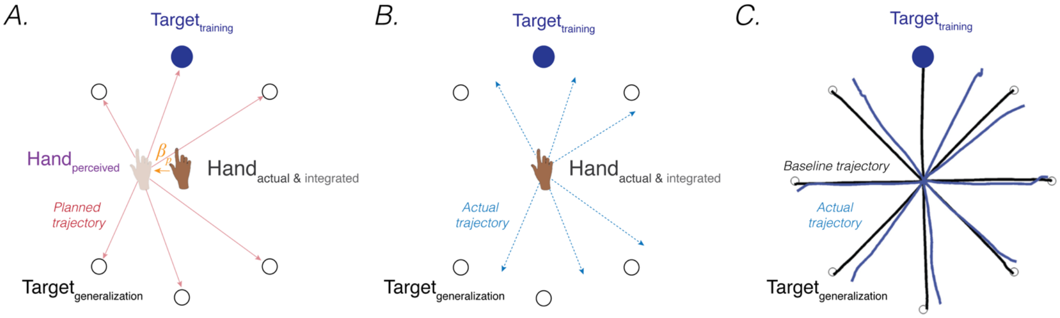

Figure 3.5. Proprioceptive shift at the start position explain patterns of generalization following a visuomotor rotation. **A)** Planned movement trajectories are formed by participants planning to make a movement initiated at their perceived hand position to the target location (red solid lines). The perceived hand position is assumed to be biased by a proprioceptive shift (β_p). **B)** The predicted generalization pattern of the proprioceptive re-alignment model (dashed blue lines; the planned trajectory is initiated from the actual/integrated hand position at the start position). **C)** Pattern of generalization assessed during no-feedback generalization trials following training with a 45° CCW rotation in one direction (upward). Black lines are baseline trajectories; blue lines are generalization trajectories. Note match of observed generalization pattern with predicted pattern shown in B), with some trajectories deviated in the clockwise direction, others in the counterclockwise direction, and no change in heading for the reaches along the horizontal meridian. Figure adapted from Figure 5a in Taylor et al, 2013.

Feature 1, Corollary 3: Implicit adaptation is correlated with the proprioceptive shift induced by passive movements

Perturbed feedback during passive limb movement can also drive implicit adaptation. A striking demonstration of this comes from a study by Salomonczyk et al. (2013). In the exposure phase (Figure 3.6A), the participant's arm was passively moved along a constrained pathway by a robotic device while a cursor moved to a remembered target location (i.e., the target disappeared when the robot-controlled movement started). Across trials, the passive movement of the arm was gradually rotated away from the cursor pathway over trials, eliciting an increasingly large discrepancy between the feedback cursor and perceived motion of the hand. When asked to report their hand position, the participants showed a proprioceptive shift of around 5° towards the visual cursor, comparable to that observed following active movements with perturbed visual feedback in a standard visuomotor rotation paradigm. After the passive perturbation phase, participants were instructed to actively reach to the visual target. These movements showed a motor aftereffect, deviating in the direction opposite to the cursor rotation. Moreover, the size of the aftereffect was correlated with the magnitude of the proprioceptive shift (Figure 3.6B). That is, participants who showed a greater proprioceptive shift towards the visual cursor also showed a stronger motor aftereffect.

PReMo can also account for the correlation between a passively-induced proprioceptive shift and the magnitude of implicit adaptation. The proprioceptive shift arises from a discrepancy between the *integrated* position of the visual cursor (x_v^I; the integration of the actual cursor position and expectation due to the motor command; Eq 3.6) and the *integrated* position of the hand (x_p^I; the integration of the actual hand position and the expectation from the motor command; Eq 3.5). When the hand is passively moved towards a predetermined location, sensory expectations from a motor command are absent. Therefore, the *integrated* positions of the cursor and hand correspond to their *actual* positions. As the integrated (actual) hand is passively and gradually rotated away from the cursor feedback (clamped at the target location), a discrepancy is introduced between the integrated positions. This visuo-proprioceptive discrepancy results in a proprioceptive shift of the integrated hand towards the integrated cursor position, and vice versa.

In contrast, visuo-centric models do not provide an account of how the sensorimotor system would be recalibrated in the absence of movement. Moreover, in this context, adaptation would not be expected given that the visual error was zero (i.e., the cursor always moved directly to the target).

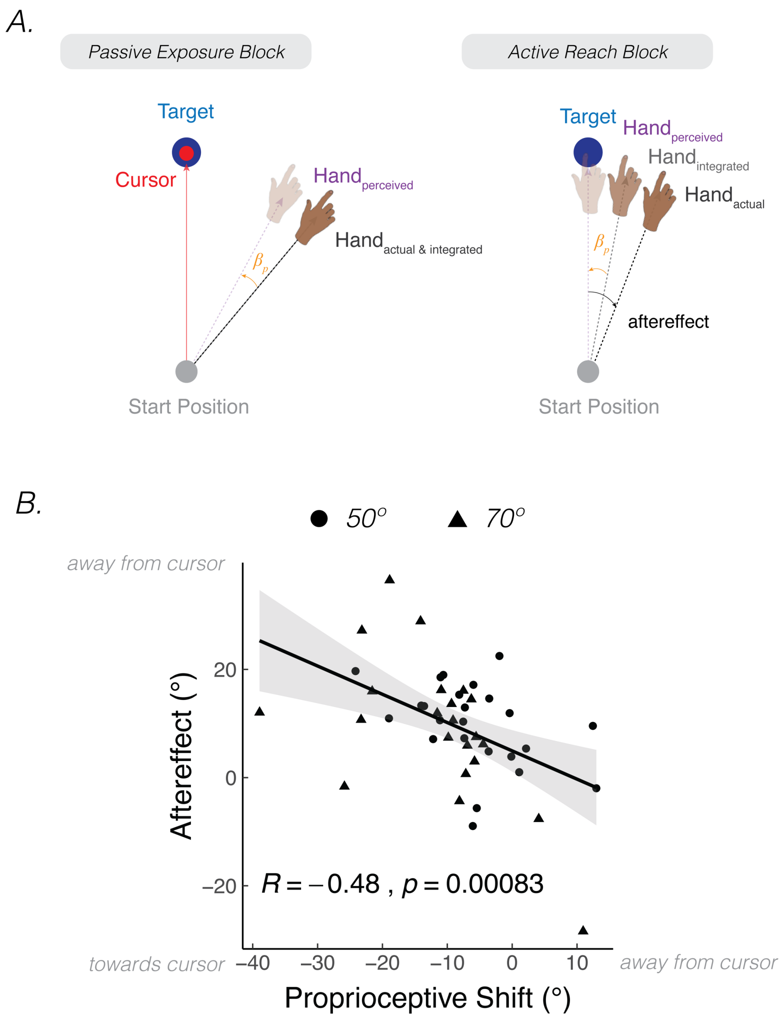

Figure 3.6. Aftereffects are elicited after passive exposure to a visuo-proprioceptive discrepancy. **A)** In Salomonczyk et al (2013), the hand was passively moved by a robot during the exposure block, with a gradual perturbation introduced that eventually reached 50° or 70° from the target (between-participant design). Simultaneous online visual feedback was provided, with the cursor moving directly to the target position. An aftereffect was measured during the active reach block in which the participant was instructed to reach directly to the target without visual feedback. **B)** Magnitude of shift in perceived hand position assessed during the passive exposure block was correlated with the motor aftereffect (Dots = 50° group; Triangles = 70° group). The more negative values on x-axis indicate a larger proprioceptive shift towards the target. The larger values on the y-axis indicate a larger motor aftereffect. Figure adapted from Figure 5 of Salomonczyk et al, 2013.

Feature 1, Corollary 4: Proprioceptive shift and implicit adaptation are both attenuated when visual feedback is delayed.

Timing imposes a powerful constraint on implicit adaptation: Delaying the visual feedback by as little as 50-100 ms can markedly reduce the rate of adaptation (Held, Efstathiou, and Greene 1966; Held and Durlach 1992; Kitazawa, Kohno, and Uka 1995). Indeed, evidence of implicit adaptation may be negligible if the visual feedback is delayed by more than 2s (Kitazawa, Kohno, and Uka 1995; Brudner et al. 2016). The attenuating effect of delayed visual feedback has been attributed to temporal constraints associated with cerebellar-dependent implicit adaptation. Specifically, while the cerebellum generates sensory predictions with exquisite resolution, the temporal extent of this predictive capability is time-limited, perhaps reflecting the kind of temporal delays that would be relevant for a system designed to keep the sensorimotor system calibrated (Miall et al. 2007; D. M. Wolpert and Miall 1996; D. M. Wolpert, Miall, and Kawato 1998; Keele and Ivry 1990). Delaying the visual feedback would presumably result in a weaker sensory prediction error, either because of a misalignment in time between the predicted and actual sensory feedback or because the sensory prediction fades over time. The consequence of this delay would be attenuated implicit adaptation.

Although we have not included temporal constraints in PReMo, it has been shown that delayed visual feedback also attenuates the proprioceptive shift; as such, the model would predict reduced adaptation since the signal driving adaptation is smaller (Eq 3.4, 3.6, 3.8). In visuomotor adaptation studies, the proprioceptive shift is reduced by ~30% for participants for whom the visual feedback on reaching trials was delayed by 750 ms, relative to those for whom the feedback was not delayed (Debats and Heuer 2020b; Debats, Heuer, and Kayser 2021). A similar phenomenon is seen in a completely different task used to study proprioceptive shift, the rubber hand illusion (Botvinick and Cohen 1998; Longo et al. 2008; Makin, Holmes, and Ehrsson 2008). Here timing is manipulated by varying the phase relationship between seeing a brush move along the rubber hand and feeling the brush against one's own arm: When the two sources of feedback are out of phase, participants not only report less ownership of the rubber hand (indexed by subjective reports), but also exhibit a smaller shift in their perceived hand position towards the rubber hand (Rohde, Di Luca, and Ernst 2011; Shimada, Fukuda, and Hiraki 2009).

While studies on the effect of delayed feedback hint at a relationship between proprioceptive shift and implicit adaptation, the supporting evidence is indirect and based on inferences made across several different studies. Future research is required to directly test whether the temporal constraints known to impact implicit adaptation also apply to proprioceptive shift.

Feature 1, Corollary 5: Proprioceptive shift and implicit adaptation are attenuated by awareness of the visual perturbation.

Although we have emphasized that adaptation is an implicit process, one that automatically occurs when the perceived hand position is not aligned with the desired hand position, there are reports that this process is attenuated when participants are aware of the visual perturbation. For example, Neville and Cressman (2018) found that participants exhibited less implicit adaptation (indexed by the motor aftereffect) when they were fully informed about the nature of visuomotor rotation and the strategy required to offset the rotation (see also, (Benson, Anguera, and Seidler 2011); but see, (Werner et al. 2015)). Relative to participants who were uninformed about the perturbation, the extent of implicit adaptation was reduced by ~33%. This attenuation has been attributed to plan-based generalization whereby the locus of implicit adaptation is centered on the aiming location and not the target location (Day et al. 2016; McDougle, Bond, and Taylor 2017; Schween, Taylor, and Hegele 2018). By this view, the attenuation is an artifact: It is only reduced when probed at the original target location, since this position is distant from the center of the generalization function. Alternatively, if adaptation and aiming are seen as competitive processes, any increase in strategic re-aiming would be expected to damp down the contribution from the adaptation system (Albert et al. 2020).

For the present purposes, we note that none of the preceding accounts refer to a role of proprioception. However, Debats and Heuer (2020a) have shown that awareness of a visuomotor perturbation attenuates the size of the proprioceptive shift (Debats and Heuer 2020a). The magnitude of this attenuation in response to a wide range of perturbations (0° - 17.5°) was around 30%, a value similar to the degree to which implicit adaptation was attenuated by awareness in the

Neville and Cressman study. A quantitative correspondence in the effect of awareness on proprioceptive shift and implicit adaptation is predicted by PReMo (Eq 3.14).

Taken together, there is some, albeit relatively thin, evidence that the proprioceptive shift and implicit adaptation may be attenuated by awareness. PReMo provides motivation for further research on this question, both to clarify the impact of awareness on these two phenomena and to test the prediction that awareness would affect proprioceptive shift and adaptation in a correlated manner.

Feature 2. Non-monotonic function of perceived hand position following introduction of visual perturbation

A core feature of PReMo is that the error signal is the difference between perceived hand position and desired hand position. Perceived hand position is rarely measured, perhaps because this variable is not relevant in visuo-centric models. When it is measured (e.g., in studies measuring proprioceptive shift), the data are usually obtained outside the context of adaptation (Cressman and Henriques 2010). That is, these proprioceptive assays are taken before and after the block of adaptation trials, providing limited insight into the dynamics of this key component of PReMo: the perceived hand location *during* implicit adaptation.

We conducted a study to probe the time course of perceived hand position in a continuous manner. Participants reached to a target and received 15° clamped visual feedback. They were asked to maintain their terminal hand position after every reach and provide a verbal report of the angular position of their hand (Figure 3.7; note that this verbal report indexes the participant's perceived hand position, x_p^{per}; this measure is not the same as proprioceptive shift, β_p) (Jonathan Sanching Tsay, Parvin, and Ivry 2020) [Footnote 3.5: The original intent of the experiment was to directly test participant's perceived hand position during adaptation, seeking to confirm the common assumption that participants are unaware of the effects of adaptation. The results of the study, especially the non-monotonic shape of the hand report function, inspired the development of PReMo.]. Surprisingly, these reports followed a striking, non-monotonic pattern. The initial responses were biased towards the clamped visual feedback by ~5°, but then reversed direction, gradually shifting *away* from the clamped visual feedback and eventually plateauing at around 2° on the opposite side of the actual target position (Figure 3.7B).

The shape and dynamics of this function are readily accounted for by PReMo. The initial shift towards the clamp is consistent with the size and rapid time course of the proprioceptive shift (Ruttle, Hart, and Henriques 2021; Ruttle, 't Hart, and Henriques 2018). It is this shift, a consequence of crossmodal recalibration between vision and proprioception, which introduces the proprioceptive error signal that drives adaptation (Eq 3.8). This error signal results in the hand moving in the opposite direction of the clamp in order to counter the perceived proprioceptive error. This, in turn, will result in a corresponding change in the perceived hand position since it is determined in part by the actual hand position (Eq 3.4 & 3.6). As such, the perceived hand location gradually converges with the perceived target location.

Intriguingly, the perceived hand position does not asymptote at the actual target location, but rather overshoots the target location by ~1°. This overshoot of the perceived hand position is also accounted for by PReMo. During exposure to the rotated visual feedback, not only is the perceived location of the cursor shifted away from the actual cursor position due to cross-sensory recalibration, but this shift is assumed to be a generic shift in visual space, not specific to just the cursor (Simani, McGuire, and Sabes 2007) (see Feature 1, Corollary 2 above). As such, the perceived location of the target is shifted away from the cursor (Figure 3.7A-B). Indeed, the overshoot provides a measure of the magnitude of this visual shift, given the assumption that behavior will asymptote when the proprioceptive error is nullified (i.e., when the perceived hand position corresponds to the desired hand position: the perceived target location).

Notably, the putative 1° of visual shift inferred from the PReMo parameter fits is consistent with empirical estimates of a visual shift induced by a visuo-proprioceptive discrepancy (M. Rand and Heuer 2019a; Simani, McGuire, and Sabes 2007). The convergence between measures obtained from very different experimental tasks supports a surprising feature of PReMo, namely that the final perceived hand position will be displaced from the actual target location. That being said, a more direct test would be to modify the continuous report task, asking participants to report the (remembered) location of the target rather than the hand.

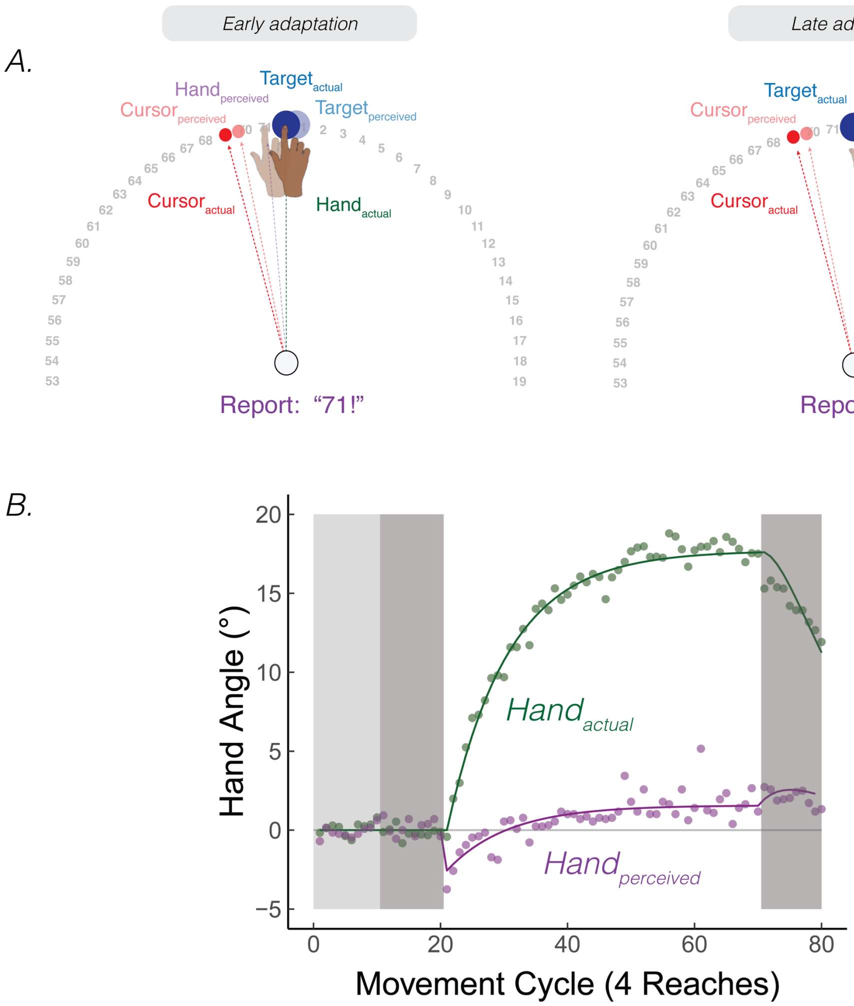

Figure 3.7. Continuous reports of perceived hand position during implicit adaptation. **A)** On each trial, participants reached to a target (blue dot) with and received 15° clamped visual feedback (red dot). After each reach, a number wheel appeared on the screen, prompting the participant to verbally report the angular position of their (unseen) hand. Participants perceived their hand on the left side of the target, shifted towards the clamped visual cursor early in adaptation. The left side shows the state of each variable contributing to perceived hand position right after the introduction of the clamp and the right side shows their states late in the adaptation block. **B)** After baseline trials (light grey = veridical feedback, dark grey = no feedback), participants exhibited 20° of implicit adaptation (green) while the hand reports (purple) showed an initial bias towards the visual cursor, followed by a reversal, eventually overshooting the target by ~2°. Lines denote

model fits of the proprioceptive re-alignment model ($R^2 = 0.995$). Figure adapted from Figure 2 of Tsay et al, 2020.

Feature 3. The effect of proprioceptive uncertainty on implicit adaptation

The preceding sections focused on how a proprioceptive shift biases the perceived hand position away from the movement goal, eliciting a proprioceptive error that drives implicit adaptation. Another factor influencing implicit adaptation is the variability in perceived hand location, i.e., proprioceptive uncertainty. This is also estimated from the psychometric function obtained from subjective reports of sensed hand position. If obtained during adaptation, the shift in perceived hand position would impact the estimates of variability. As such, a cleaner approach is to measure proprioceptive uncertainty prior to adaptation (Figure 3.3). As shown in several experiments, greater proprioceptive uncertainty/variability is associated with a greater extent of implicit adaptation (Figure 3.3H, I, J).

As with measures of proprioceptive shift, conventional visuo-centric models of implicit adaptation do not account for the relationship between proprioceptive uncertainty and the magnitude of adaptation. In these models, the extent of implicit adaptation reflects the point of equilibrium between learning and forgetting from a *visual* error and do not specify how the extent of implicit adaptation may be related to proprioception. In contrast, PReMo predicts that proprioceptive variability will be negatively correlated with implicit adaptation (Eq 3.14). When there is greater uncertainty in the proprioceptive system, the perceived hand position is more biased by the location of sensory expectations from the motor command (i.e., the visual target, Eq 3.4). Therefore, participants with greater uncertainty in proprioception would require a greater change in their actual hand position to bring their perceived hand position into alignment with the perceived target.

Feature 4. The effect of visual uncertainty on implicit adaptation.

Visual uncertainty can also affect motor adaptation. In a seminal study by Burge et al (2008), the visual feedback in a 6° (small) visuomotor rotation task was provided in the form of a sharply defined cursor (low uncertainty) or a diffuse Gaussian blob (high uncertainty). In the high uncertainty condition, motor adaptation was attenuated both in rate and asymptotic value. The authors interpreted this effect through the lens of optimal integration (Burge, Ernst, and Banks 2008; Ernst and Banks 2002), where the learning rate is determined by the participant's confidence in their estimate of the sensory prediction and feedback. When confidence in either is low, the learning rate will be decreased; thus, the added uncertainty introduced by the Gaussian blob reduces the learning rate and, consequently, the asymptotic value of total adaptation. By this view, visual uncertainty should attenuate adaptation for all visual error sizes. [Footnote 3.6*:* Since Burge et al (2008) used a standard visuomotor rotation task where visual feedback is contingent on the participant's behavior, the learning function may also include a contribution from strategy use. This motivated us to use the clamped feedback task in a re-examination of the effect of visual uncertainty on implicit adaptation (Tsay et al (2021)].

PReMo offers an alternative interpretation of these results. Rather than assume that visual uncertainty impacts the strength of the error signal, PReMo postulates that visual uncertainty indirectly affects implicit adaptation by influencing the magnitude of the proprioceptive shift. This hypothesis predicts that the impact of visual uncertainty may depend on the visual error size.

To explain this prediction, consider Eq 3.14, the core equation specifying the relationship between the upper bound of implicit adaptation and the degree of the proprioceptive shift, β_p. When the visual error is small, the proprioceptive shift, being a fraction of the integrated hand/cursor positions will be below the level where it saturates (Eq 3.8). As such, we can substitute β_p with the expression, $\eta_p(x_{v,t}^I - x_{p,t}^I)$, that is, a fraction of the difference between integrated positions of the hand and cursor (Eq 3.18):

$$x_p^{UB} = \frac{-\eta_p(x_v^I - x_p^I)(\sigma_u^2 + \sigma_p^2)}{\sigma_u^2} \quad (3.18)$$

Furthermore, we can substitute the integrated positions of the hand ($x_{p,t}^I$) and the visual cursor ($x_{v,t}^I$) from Eq 3.4 and Eq 3.5, respectively, to relate the upper bound of implicit adaptation with uncertainty in proprioception (σ_p^2), vision (σ_v^2), and the sensory prediction (σ_u^2). For the sake of simple exposition, we assumed that visual shifts are negligible and that participants continue to aim directly to the target ($G_t = 0$), but the same logic would apply if visual shifts were non-zero (Eq 3.19):

$$x_p^{UB} = \frac{\sigma_u^2 + \sigma_p^2}{(\sigma_u^2 + \sigma_v^2)(1 - \eta_p)} x_{v,t} \quad (3.19)$$

As visual uncertainty increases, the denominator in Eq 3.19 increases, and thus, the upper bound of implicit adaptation decreases. More specifically, when visual uncertainty of a small visual error increases, the integrated cursor is drawn closer to the visual target (the aiming location), and, thus, closer to the integrated hand position (assumed to be near the target during early adaptation). For small errors, the discrepancy between integrated positions of the cursor and hand decreases as visual uncertainty increases. This will reduce the size of the proprioceptive shift and, consequently, result in the attenuation of implicit adaptation.

In contrast, consider the situation when the visual error is large. Now the visuo-proprioceptive discrepancy is large ($\uparrow x_v^I - x_p^I$) and we can assume the proprioceptive shift will be at the point of saturation ($\beta_{p,sat}$). As such, the upper bound of implicit adaptation will no longer depend on visual uncertainty (see Eq 3.14) and, thus, implicit adaptation will not be attenuated by visual uncertainty. In summary, PReMo, predicts an interaction between error size and the effect of visual uncertainty on adaptation.

The results of an experiment in which we varied visual uncertainty and error size are consistent with this prediction. To have full control over the size of the error, we used the clamped feedback method. We varied visual uncertainty (cursor = certain feedback, Gaussian cloud = uncertain feedback) and the size of the visual error (3.5° = small error, 30° = large error) in a 2x2 design (Figure 3.8A). Visual uncertainty attenuated implicit adaptation when the error size was small (3.5°), convergent with the results of Burge et al (2008) (Figure 3.8B). However, visual uncertainty did not attenuate implicit adaptation when the error size was large (30°) (Van Beers, Sittig, and Gon 1999; Robert J. van Beers, Baraduc, and Wolpert 2002), yielding the predicted interaction.

It is possible that the Gaussian cloud led to lower adaptation because the added noise induced more "successful" trials, given previous work showing that implicit adaptation is attenuated when the visual cursor intersects the target (Leow et al. 2018, 2020; Jonathan S. Tsay, Haith, Ivry, et al. 2022). This concern was one of the reasons why we blanked the target at reach onset in Tsay et al 2020. Nonetheless, more direct evidence that the attenuation stems from uncertainty (and not reward) comes from an unpublished study involving participants with low vision and matched controls, allowing a test of the effect of uncertainty when it comes from an intrinsic source (the individual) rather than manipulating an extrinsic source (the Gaussian cloud) (Jonathan S. Tsay, Tan, Chu, et al. 2022). The results exhibit the same interaction, with visual uncertainty due to low vision attenuating implicit adaptation for small errors but not large errors (despite visual feedback being equated in both groups).

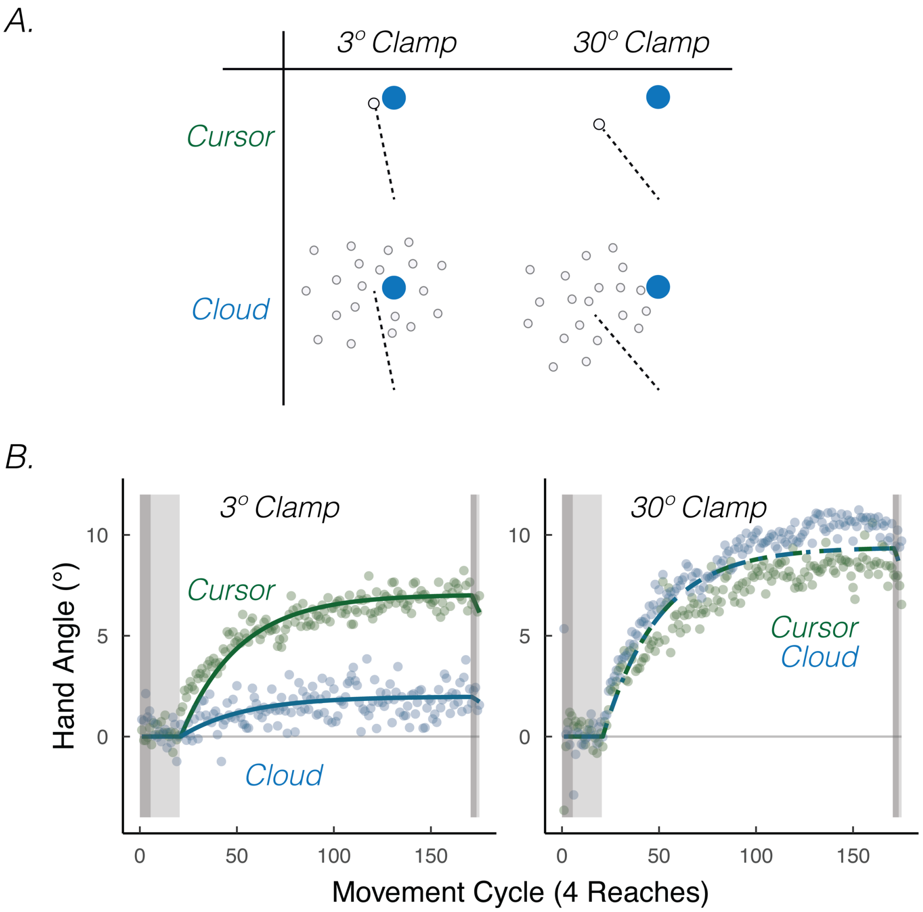

Figure 3.8. Visual uncertainty attenuates implicit motor adaptation in response to small visual errors, but not large visual errors. **A)** Experimental design in Tsay et al (2021). Participants made reaching movements in a similar setup as Figure 3.1A. Feedback was provided as a small 3.5° visual clamp or large 30° visual clamp, either in the form of a cursor or cloud (2x2 between-subject factorial design). **B)** Tsay et al (2021) Results. Implicit adaptation was attenuated by the cloud feedback when the clamp size was 3.5° but not when the clamp size was 30°. Lines denote model fits of the proprioceptive re-alignment model ($R^2 = 0.929$). Figure adapted from Figure 3 of Tsay et al, 2021.

Feature 5. The effect of sensory prediction uncertainty on implicit adaptation

All models of implicit adaptation require a comparison of predicted and observed feedback to derive an error signal. In the previous section, we discussed how PReMo can account for attenuated adaptation observed in the face of noisy feedback – a variable that is easy to manipulate. In this section we consider the effects of noisy predictions, a latent measure in the model, and one that is difficult to manipulate.

Extrinsic and *intrinsic* sources of variability have been posited to impact the strength of the predicted sensory consequences of a movement. Extrinsic variability, defined here as variability in movement outcomes that are not attributable to one's own motor output, will reduce one's ability to make accurate sensory predictions. Such effects are usually simulated in the lab by varying the perturbation across trials. For example, Albert et al (2021) compared implicit adaptation (i.e., indexed by motor aftereffects during the washout phase where participants were instructed to forgo any strategy use) in two groups of participants, one exposed to a constant 30° visuomotor rotation and a second exposed to a variable rotation that, across trials, averaged 30° (SD = 12°) (Experiment 7 in Albert et al, 2021). Aftereffects were attenuated by around 30% in the latter condition. From the perspective of PReMo, this effect could be attributed to increased sensory prediction noise.

However, these results should be interpreted with caution: Other studies have found no effect of perturbation variability on adaptation (Avraham, Keizman, and Shmuelof 2020; Butcher et al. 2017) or even an amplified effect on learning from increased perturbation variability (Burge, Ernst, and Banks 2008). Moreover, the attenuation of adaptation due to uncertainly can emerge from differential sampling of error space relative to a condition with low uncertainty (Wang et al. 2022), even when the learning rate is identical for the two conditions. Given the mixed results on this issue (also see: (Hutter and Taylor 2018)), it is unclear if extrinsic variability contributes to the strength of the sensory prediction.

We define variability as noise arising within the agent's nervous system. High variability will, over trials, decrease the accuracy of the sensory predictions. Indeed, an impairment in generating a sensory prediction provides one mechanistic account of why individuals with cerebellar pathology show attenuated sensorimotor adaptation across a range of tasks (Martin et al. 1996; Hadjiosif et al. 2014; Izawa, Criscimagna-Hemminger, and Shadmehr 2012; Tseng et al. 2007; Schlerf et al. 2013; Parrell et al. 2021; Gibo et al. 2013; Fernandez-Ruiz et al. 2007; Donchin et al. 2012). From the perspective of a state-space model, this impairment is manifest as a lower learning rate (Figure 3.9), although this term encompasses a number of processes. PReMo suggests a specific interpretation: Noisier sensory predictions will result in the actual hand position having a relatively larger contribution to the perceived location of their hand. As such, a smaller change in actual hand position would be required to nullify the proprioceptive error (Eq 3.14), effectively lowering the upper bound of implicit adaptation.

Evidence from a number of different tasks is consistent with the hypothesis that cerebellar pathology is associated with noisier sensory predictions (Gaffin-Cahn, Hudson, and Landy 2019; Bhanpuri, Okamura, and Bastian 2013; Therrien and Bastian 2019; Weeks, Therrien, and Bastian 2017b). Nonetheless, we recognize that cerebellar pathology may disrupt other processes relevant for implicit adaptation. For example, the disease process may result in a lower (generic) learning rate or core proprioceptive variables. However, with respect to the latter, various lines of evidence indicate that proprioception, at least those aspects highlighted in PReMo, are not impacted by cerebellar pathology. First, these individuals do not exhibit impairment on measures of proprioception obtained without volitional movement (i.e., under static conditions) (Bhanpuri, Okamura, and Bastian 2013). Second, the magnitude of the proprioceptive shift in cerebellar patients is comparable to that observed in control participants (Henriques et al. 2014). Third, proprioceptive variability appears to be comparable between individuals with cerebellar pathology and matched controls (Weeks, Therrien, and Bastian 2017b, 2017a; Bhanpuri, Okamura, and Bastian 2013).

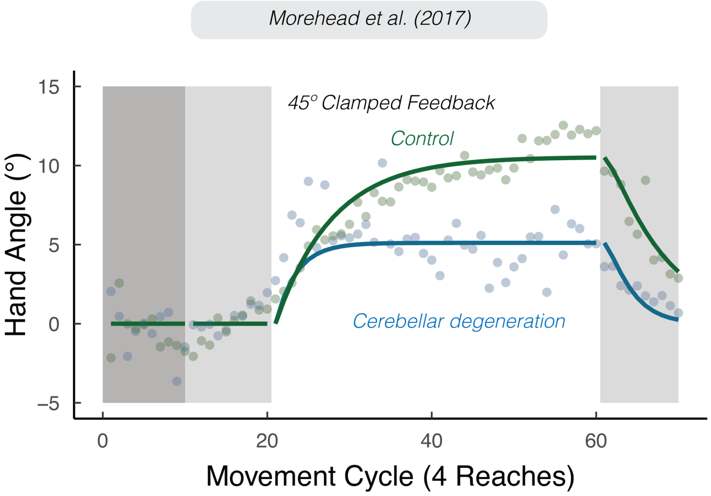

Figure 3.9. Sensory prediction uncertainty attenuates implicit adaptation. Attenuated adaptation in individuals with cerebellar degeneration compared to matched controls in response to 45° clamped feedback. Lines denote model fits of the proprioceptive re-alignment model ($R^2 = 0.897$). Figure adapted from Figure 3a of Morehead et al, 2017.

Feature 6: Generalizing the proprioceptive re-alignment model from visuomotor to force-field adaptation

Implicit adaptation is observed over a wide range of contexts, reflecting the importance of keeping the sensorimotor system precisely calibrated. In terms of arm movements, force-field perturbations have provided a second model task to study adaptation (Shadmehr, Mussa-Ivaldi, and Bizzi 1993). In a typical task, participants reach to a visual target while holding the handle of a robotic device. The robot is programmed such that it exerts a velocity-dependent force in a direction orthogonal to the hand's movement. Over the course of learning, participants come to exert an opposing time-varying force, resulting in a trajectory that once again follows a relatively straight path to the target.

In contrast to visuomotor adaptation tasks, there is no manipulation of sensory feedback in a typical force-field study; people see and feel their hand exactly where it is throughout the experiment. Nevertheless, several studies have reported sensory shifts following force-field adaptation (Figure 3.10A). In particular, the perceived hand position becomes shifted in the direction of the force-field (Mattar, Darainy, and Ostry 2013; Ohashi, Gribble, and Ostry 2019; Ostry et al. 2010). [Footnote 3.7: At odds with this pattern, Haith et al. (A. Haith et al. 2009) reported a proprioceptive shift during force-field adaptation but in the direction opposite to the applied force. However, this study only involved a leftward force-field. The rightward shifts in perceived hand position may be due to a systematic rightward proprioceptive drift, a phenomenon observed in right-handed participants with repeated reaches, with or without feedback (Brown, Rosenbaum, and Sainburg 2003a, 2003b).].

PReMo can account for the shift in perceived hand position in the direction of the force-field. Consider the situation where a force-field pushes the hand to the right, an effect that is maximal at peak velocity for a velocity dependent force-field (Figures 3.10C-F). An estimate of hand position will involve intramodal integration of sensory feedback signals (the cursor for vision, the actual hand position for proprioception) and the sensory prediction (i.e., a straight trajectory of the hand towards the target). This will result in an integrated representation of the hand and cursor trajectory as shifted towards the target. Importantly, given that proprioceptive variability is greater than visual variability (Van Beers, Sittig, and Gon 1999; Robert J. van Beers, Baraduc, and Wolpert 2002), this shift towards the target is likely greater for the hand than the cursor. The visuo-proprioceptive discrepancy between integrated positions will result in crossmodal calibration, with the integrated hand and cursor positions shifted towards each other, forming the perceived hand and cursor positions, respectively (Figure 3.10E). Thus, there will be a small but systematic shift in the perceived location of the hand in the direction of the force-field perturbation.

Models of force-field adaptation suggest that the error signal driving adaptation is the deviation between the ideal and actual forces applied during the movement. This can be estimated based on the deviation of the hand's trajectory from a straight line (Donchin, Francis, and Shadmehr 2003). These models are agnostic to whether this error is fundamentally visual or proprioceptive since the position of the cursor and hand are one and the same. That is, the error could be visual (the trajectory of the cursor was not straight towards the target) or proprioceptive (the trajectory of the hand did not feel straight towards the target). Notably, neurologically healthy and congenitally blind individuals can adapt to a force-field perturbation without the aid of vision, with their perceived hand position relying solely on proprioceptive input from the moving limb (DiZio and Lackner 2000). Similarly, deafferented individuals also adapt in response to force-field perturbations. Presumably their perceived hand position is dependent on the position of the feedback cursor (Miall et al. 2018; Sarlegna et al. 2010). Furthermore, when opposing visual and proprioceptive errors are provided, aftereffects measured during the no-feedback block after adaptation are in the direction counteracting the proprioceptive error instead of the visual error (Hayashi, Kato, and Nozaki 2020). As such, we suggest that force-field adaptation may be fundamentally proprioceptive. Consistent with the basic premise of PReMo, the difference between the perceived and desired hand position constitutes the error signal to drive force-field adaptation, a process that can operate in the absence of visual feedback. Strikingly, Matter et al (2013) found that the degree in which participants adapt to the forcefield is correlated with the amount of proprioceptive shift in the direction of the force-field, strengthening the link between the sensory and motor changes that arise during force-field adaptation (also see Feature 1).

In summary, PReMo offers a unified account of the motor and perceptual changes observed during force-field and visuomotor adaptation – both of which place emphasis on participants reaching directly to a target. The applicability of the model for other types of movements remains to be seen. Proprioception seems quite relevant for locomotor adaptation where the goal of the motor system is to maintain gait symmetry (Reisman et al. 2007; Morton and Bastian 2006; Rossi et al. 2019): The misalignment between the desired and perceived gait might serve as a proprioceptive error, triggering implicit locomotive adaptation to restore its symmetry. Indeed, for locomotor adaptation, it is unclear what sort of visual information might be used to derive an error signal. In contrast, the goal in saccade adaptation is fundamentally visual, to align the eye on a target (Grüsser 1983; Groh and Sparks 1996; Pélisson et al. 2010). The oculomotor system appears to rely on a visual error signal to maintain calibration (Lewis et al. 2001; Noto and Robinson 2001; Wallman and Fuchs 1998).

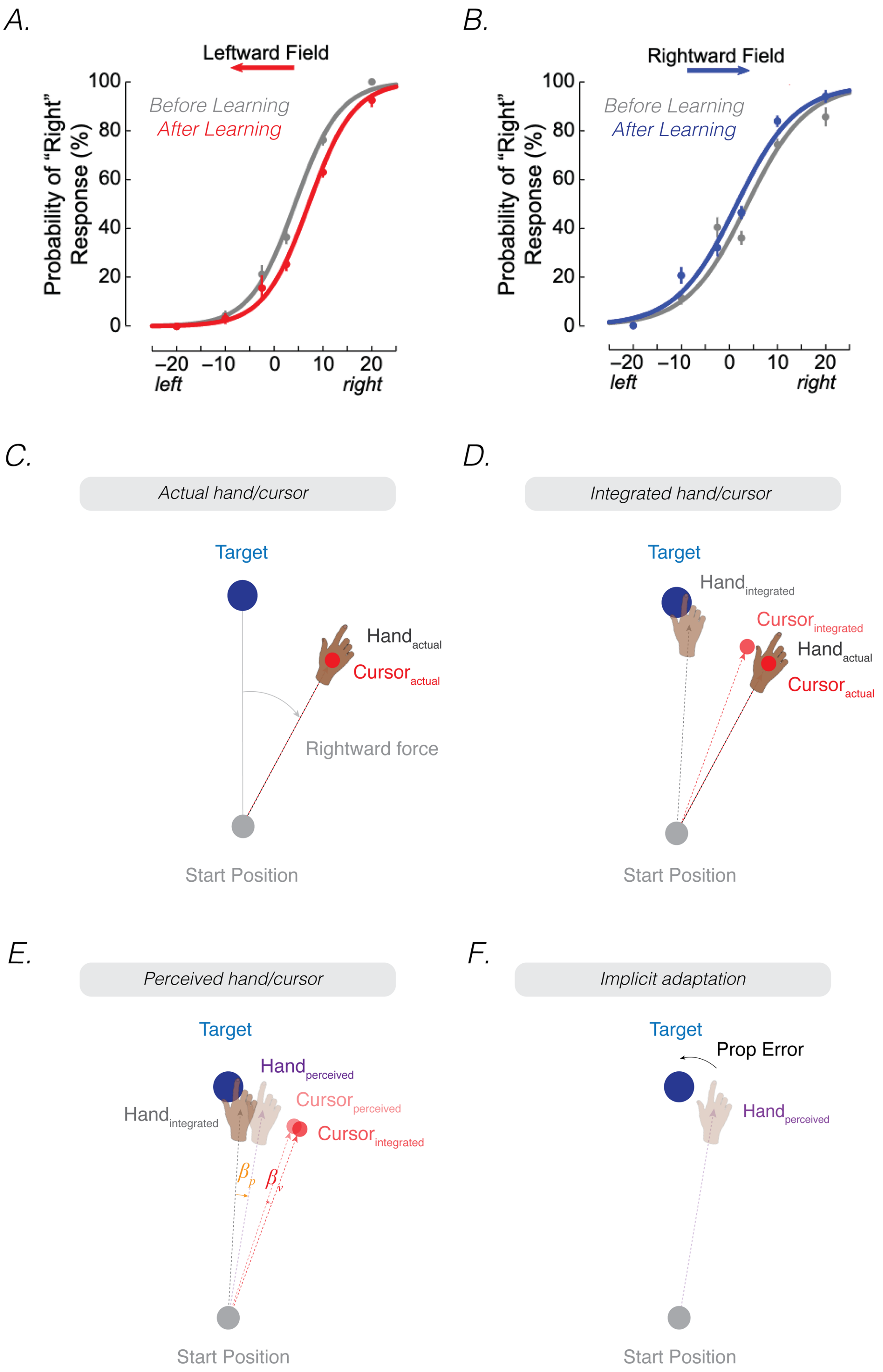
A.
Leftward Field
Before Learning
After Learning
Probability of "Right" Response (%)
100
80
60
40
20
0
−20
−10
0
10
20
left
right
B.
Rightward Field
Before Learning
After Learning
Probability of "Right" Response (%)
100
80
60
40
20
0
−20
−10
0
10
20
left
right
C.
Actual hand/cursor
Target
Hand actual
Cursor actual
Rightward force
Start Position
D.
Integrated hand/cursor
Target
Hand integrated
Cursor integrated
Hand actual
Cursor actual
Start Position
E.
Perceived hand/cursor
Target
Hand perceived
Cursor perceived
Hand integrated
Cursor integrated
βp
βv
Start Position
F.
Implicit adaptation
Target
Prop Error
Hand perceived
Start Position

Figure 3.10. The proprioceptive re-alignment model explains sensory and motor changes during force-field adaptation. **A, B)** Participants' perceptual judgments of actual hand position are biased in the direction of the recently experienced force-field. Figure adapted from Figure 2 of Ostry et al, 2010. These psychometric curves were obtained using a staircase method performed before and after force-field adaptation: the participant made center-out reaching movements toward a target. Force channels pushed the participant's hand towards the left or right of the target by varying amounts. At the end of the movement, the participant judged the position of their hand relative to the target (left or right). Each participant's shift quantified as the change in the point of subjective equality (PSE). The shift in the PSE in panels A and B indicate that the perceived hand position following force-field adaptation was shifted in the direction of the force-field. **C)** Upon introduction of the force-field perturbation, the hand and (veridical) cursor are displaced in the direction of the force-field, especially at peak velocity. Note that the hand and cursor positions are illustrated at the endpoint position for ease of exposition. **D)** Assuming that proprioceptive uncertainty is greater than visual uncertainty, the integrated hand position would be closer to the target than the integrated cursor position due to principles of optimal integration. **E)** The two integrated positions then mutually calibrate, resulting in a proprioceptive shift (β_p) of the integrated hand towards the integrated cursor position, and a visual shift (β_v) of the integrated cursor position towards the integrated hand position, forming the perceived hand and perceived cursor locations. **F)** The proprioceptive error (mismatch between the perceived hand position and the target) drives adaptation, a force profile in the opposition direction of the force-field.

Concluding remarks

In the current article, we have proposed a model in which proprioception is the key driver of implicit adaptation. In contrast to the current visuo-centric zeitgeist, we have argued that adaptation can be best understood as minimizing a proprioceptive error, the discrepancy between the perceived limb position and its intended goal. On ecological grounds, our model reframes adaptation in terms of the primary intention of most manual actions, namely, to use our hands to interact and manipulate objects in the world. In visuo-centric models, the central goal is achieved in an indirect manner, with the error signal derived from visual feedback about the movement outcome being the primary agent of change. Empirically, the proprioceptive re-alignment model accounts for a wide range of unexplained, and in some cases, unintuitive phenomena: Changes in proprioception observed during both visuomotor and force-field adaptation, phenomenal experience of perceived hand position, the effect of goal and sensory uncertainty on adaptation, and saturation effects observed in the rate and extent of implicit adaptation.

To be clear, the core ideas of PReMo are framed at Marr's 'computational' and 'algorithmic' levels of explanation. At the computational level, we seek to explain *why* implicit adaptation is elicited (to align felt hand position with the movement goal); at the algorithmic level, we ask *how* implicit adaptation is instantiated (felt hand position being a combination of vision, proprioception of the moving limb, and efferent information; movement goal being the perceived location of the target). We hope PReMo motivates studies that focus on the implementational level. Here we anticipate that it will be important to consider both peripheral (Dimitriou 2016) and central mechanisms (Proske and Gandevia 2012; Latash 2021) to account for the modification of multisensory representations across the course of adaptation.

It should be emphasized that, to date, much of the key evidence for PReMo comes from correlational studies; in particular, the relationship between the magnitude of adaptation and the extent and variability of induced changes in proprioception following adaptation. While studies using a wide range of methods have revealed robust correlations between measures of proprioception and adaptation, other studies have failed to find significant correlations (Cressman et al. 2021; Cressman, Salomonczyk, and Henriques 2010) (Vandevoorde and Orban de Xivry 2021). The reason for these differences is unclear but may be related to the methodological differences. For instance, when proprioception is assessed via subjective reports obtained after an active movement, it may be impossible to dissociate the relative contributions of proprioceptive variability and sensory prediction variability to perceived hand position (Izawa and Shadmehr 2011; Izawa, Criscimagna-Hemminger, and Shadmehr 2012; Synofzik, Lindner, and Thier 2008). More important, correlations of the proprioceptive data with implicit adaptation would confound these two sources of variability.

Development and validation of proprioceptive measures that do not rely on subjective reports may bypass these shortcomings. Rand and Heuer, for instance, have developed a measure of proprioception that is based on movement kinematics, without participants being aware of the assessment (M. Rand and Heuer 2019b). Using a center-out reaching task, the participants' perceived hand position after the outbound movement is inferred by the angular trajectory of the inbound movement back to the start position. A straight trajectory to the start position may indicate that the participant is fully aware of their hand position, whereas any deviation in this trajectory is inferred to reveal a proprioceptive bias. This indirect measure of proprioception shows the signature of a proprioceptive shift with a similar time course as that observed when the shift is measured in a more direct manner.

Even though each correlation, when considered in isolation, should be interpreted with caution, we believe that when considered in aggregate, PReMo provides a parsimonious explanation for a wide range of empirical phenomena. Importantly, PReMo provides sufficient detail to generate a host of qualitative and quantitative predictions based on a reasonable set of assumptions. For example, the computation of perceived hand position is based on established principles of sensory integration (Ernst & Banks, 2002) and sensory recalibration (Zaidel et al., 2011). Moreover, the key proposition of PReMo, namely that implicit sensorimotor adaptation operates to reduce a proprioceptive error, is highly ecological.

As with all correlational work, inferences about the causality are indirect and may be obscured by mediating variables. For example, instead of implicit adaptation being driven by the proprioceptive shift, it is possible that the visual error introduced by a perturbation independently drives implicit adaptation and the proprioceptive shift. By laying out a broad range of phenomena in this review, we hope to establish a benchmark for comparing the relative merits of PReMo and alternative hypotheses.

Beyond model comparison and appeals to parsimony, a more direct tack to evaluate the core proposition of PReMo would involve experimental manipulations of proprioception. Brain stimulation methods have been used to perturb central mechanisms for proprioception (Armenta Salas et al. 2018; Balslev et al. 2004; Balslev, Miall, and Cole 2007; H. Block, Bastian, and Celnik 2013; Miall et al. 2007) and tendon vibration has been a fruitful way to perturb proprioceptive signals arising from the periphery (Bernier et al. 2007; Gilhodes, Roll, and Tardy-Gervet 1986; Goodwin, McCloskey, and Matthews 1972; Manzone and Tremblay 2020; R. Roll, Velay, and Roll 1991; Bock and Thomas 2011; Layne, Chelette, and Pourmoghaddam 2015; Bard et al. 2011). PReMo would predict that implicit adaptation would be enhanced with greater proprioceptive bias induced by tendon vibration to one muscle group (e.g., vibration to the biceps resulting in illusory elbow extension) and greater proprioceptive uncertainty via vibrating opposing muscle groups (e.g., vibration to biceps and triceps adding noise to peripheral proprioceptive afferents).

Adaptation encompasses a critical feature of our motor competence, the ability to use our hands to interact and manipulate the environment. As experimentalists we introduce non-ecological perturbations to probe the system, with the principles that emerge from these studies shedding insight into those processes essential for maintaining a precisely calibrated sensorimotor system. This process operates in an obligatory and rigid manner, responding, according to our model, to the mismatch between the desired and perceived proprioceptive feedback. As noted throughout this review, the extent of this recalibration process is limited, likely reflecting the natural statistics of proprioceptive errors. The model does not capture the full range of motor capabilities we exhibit as humans (Listman et al. 2021). Skill learning requires a much more flexible system, one that can exploit multiple sources of information and heuristics to create novel movement patterns (Yang, Cowan, and Haith 2021). These capabilities draw on multiple learning processes that use a broad range of error and reinforcement signals (Galea et al. 2011; Shmuelof, Krakauer, and Mazzoni 2012; Jonathan S. Tsay, Kim, Saxena, et al. 2021) that may be attuned to different contexts (Heald, Lengyel, and Wolpert 2021; Avraham, Taylor, et al. 2020). While we anticipate that these processes are sensitive to multimodal inputs, it will be useful to revisit these models with an eye on the relevance of proprioception.

Open Questions

1. How general are the principles of PReMo for understanding sensorimotor adaptation in other motor domains? For example, can PReMo account for locomotor adaptation?

2. How do we reconcile PReMo's emphasis on proprioceptive error with the observation that individuals with severe proprioceptive deficits exhibit adaptation? Is this due to a compensatory process? Or the internal representation of hand position based on sensory expectancies interacting with biases from vision? Insights into this question will also be relevant for recalibrating movements when learning to use a tool, prosthetic limb, or body-augmentation devices in which the goal of the action is not isomorphic with a proprioceptive signal.

3. A core principle of PReMo is that the perceived location of the target and hand are biased by various sources of information. What is the impact of these biases on other learning processes engaged during sensorimotor adaptation tasks (e.g., use-dependent learning or strategic re-aiming)?

4. We have proposed that the impairment in adaptation associated with cerebellar pathology may arise from noisier sensory predictions, a hypothesis consistent with the view that the cerebellum is essential for predicting the proprioceptive outcome of a movement based on efference copy. Alternatively, within the framework of PReMo, the impairment might relate to a reduced learning rate, a disturbance of proprioception, or a combination of factors. Specifying the source of impairment will require experiments involving tasks that yield independent measures of these variables to constrain parameters when fitting learning functions.

5. New insights into cerebellar function have come about by considering the representation of error signals in Purkinje cells during saccade adaptation (Herzfeld et al. 2018). Can the principles of PReMo be validated neurophysiologically by examining the time course of error-related activity during adaptation. For example, in response to clamped feedback, PReMo would predict an attenuation of the error signal as proprioceptive alignment occurs whereas standard state-space models would predict little change, with the asymptote reached when the effect of the persistent error is offset by forgetting.

6. What are the implications of PReMo for physical rehabilitation of neurologic populations who are at high risk of proprioceptive impairments, such as stroke and Parkinson's disease?

Appendix

The contribution of visual shifts in PReMo

Crossmodal recalibration is a phenomenon in which two discrepant modalities exhibit a mutual attraction (Zoubin Ghahramani, Wolptrt, and Jordan 1997; Zaidel, Turner, and Angelaki 2011; Burge, Girshick, and Banks 2010; Hong, Badde, and Landy 2020). For example, after being exposed to a persistent discrepancy between visual and auditory signals conveying an object's location, the perceived location of the vision and auditory stimuli gravitate towards each other. Similarly, we would assume that that visual and proprioceptive signals are attracted towards each other in the context of a visuomotor rotation. The presence of a proprioceptive shift towards the cursor has been well-documented in the literature (Cressman and Henriques 2010, 2011). However, the evidence of a visual shift towards the hand is much weaker (e.g., see (Simani, McGuire, and Sabes 2007)), and when observed, the effect is relatively small (M. Rand and Heuer 2020; H. J. Block and Bastian 2011).

We note that visual shifts of the feedback and target play a minor role in PReMo. Implicit adaptation is driven by a proprioceptive error, the mismatch between the perceived hand position and the desired hand position (the visual target). These variables are not affected by visual shift. The effect of a visual shift comes about indirectly if one assumes that the perceived location of the feedback cursor is shifted towards the hand once the clamp is introduced. Assuming that shift is applied across the visual space, this would also shift the perceived position of the target. As such, adaptation would not cease when the hand is perceived at the true target location but rather at the perceived target location. The hand report data in Tsay et al. (2020) indicate that, at asymptote, the perceived hand position is shifted by about 1°. A shift of this size would result in a small increase of the upper bound of adaptation. Given the inconsistencies in the literature concerning a visual shift during visuomotor adaptation, it will be important to replicate these effects and more important, employ methods to directly measure perceived target position (e.g., blanking the target during the reach).

Fitting the Proprioceptive re-alignment model

Using R language's fmincon function, we started with 10 different initial sets of parameter values to estimate the parameter values that minimized the least squared error between the average data and model output. The key dependent variables were hand angle and reports of perceived hand position. The eight key parameters were σ_v (visual uncertainty), σ_p (proprioceptive uncertainty), σ_u (sensory prediction/expectation uncertainty), η_p (proprioceptive shift ratio), η_v (visual shift ratio), $\beta_{p,sat}$ (saturation of proprioceptive shift), K (learning rate), and A (rate of proprioceptive decay).

Proprioceptive shift does not correlate with proprioceptive variability

While it is reasonable to posit that proprioceptive shift and proprioceptive variability will be correlated with one another given that each variable correlates with the extent of implicit adaptation, this need not be the case: Two variables can be independent from one another, yet still both correlate with a third variable. For example, shift and uncertainty could each make positive, yet independent contributions to implicit adaptation. There are theoretical reasons, mainly from the sensory integration world to expect shift and uncertainty to be correlated. Empirically, however, several studies have found this to not be the case (Jonathan S. Tsay, Kim, Parvin, et al. 2021; Ayala, Marius 't Hart, and Henriques 2020). While noting this is a null result, these data suggest that the degree of sensory recalibration may not follow a Bayesian optimal rule in which the extent of sensory shifts are based on the relative reliabilities of each sensory signal. This hypothesis is consistent with Zaidel et al (2011) who found that visual/vestibular cross-modal recalibration did not follow Bayesian optimality principles. Instead, these two sensory modalities appear to shift towards each other in a fixed ratio manner. For these reasons, we opted to formulate the proprioceptive shift in PReMo as independent of sensory uncertainty (see Eq 3.5 & 3.6).

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