J Neurophysiol 124: 1122–1130, 2020.
First published September 9, 2020; doi:10.1152/jn.00242.2020.

RESEARCH ARTICLE | *Control of Movement*

Continuous reports of sensed hand position during sensorimotor adaptation

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Submitted 1 May 2020; accepted in final form 21 August 2020

Tsay JS, Parvin DE, Ivry RB. Continuous reports of sensed hand position during sensorimotor adaptation. *J Neurophysiol* 124: 1122–1130, 2020. First published September 9, 2020; doi:10.1152/jn.00242.2020.—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. Although it is clear that the response to clamped feedback occurs automatically, it remains unknown whether 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 toward 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.

NEW & NOTEWORTHY Sensorimotor adaptation operates in an obligatory manner. Qualitatively, subjective reports obtained after adaptation demonstrate that, in many conditions, participants are unaware of significant changes in behavior. In the present study, we quantified participants’ sensitivity to these adaptive changes by obtaining reports of hand position on a trial-by-trial basis. The results confirm that participants are largely unaware of adaptation but also reveal the subtle influence of feedback on their subjective experience.

error-based learning; motor learning; proprioception; sensorimotor adaptation

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 et al. 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 (Helmholtz 1924; Krakauer et al. 2000; Redding et al. 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.

Although the participant’s phenomenological experience after learning suggests 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 (Bond and Taylor 2015; Mazzoni and Krakauer 2006; Shmuelof et al. 2012; Taylor and Ivry 2011; Taylor et al. 2014). 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 (Taylor et al. 2014; Werner et al. 2015). 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 exhibits 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

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adaptation system, in an obligatory manner, treats the discrepancy between the target and feedback cursor as a sensory prediction error. Because 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 $\sim 20^{\circ}$, and even reach values $>45^{\circ}$ 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 females, mean age = 21, age range: 18–25) were recruited from the Berkeley, CA, 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, CA.

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; 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; see Faul et al. 2009, 2007).

Reaching task. Participants were seated at a custom-made table (Fig. 1*A*) that housed an LCD screen (53.2 cm by 30 cm, ASUS monitor) 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.

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 provided only 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 pseudorandomized 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 end point 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 (Fig. 1*B*), 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 ($\leq$8 cm), but noncontingent 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."

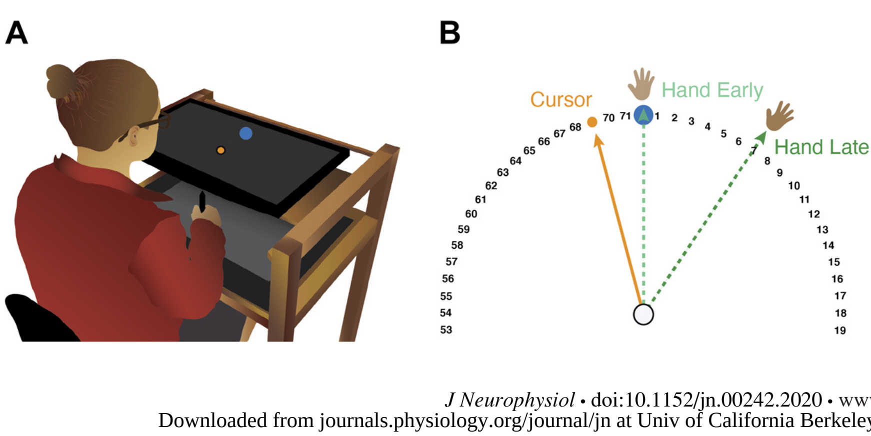

Fig. 1. Experimental methods. *A*: experimental apparatus and setup. *B*: schematic overview of the error clamp paradigm, in which the angular path of the cursor (yellow) is held constant and independent of hand movement direction (green). Dotted lines depict representative trajectories at the start (early) and end (late) of the error clamp block.

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 1 reach to each of the 4 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 that 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 six 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 toward 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 the participants' 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: 3,577 ms; without hand reports: 2,735 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° (1st trial), 270° (2nd trial), and 0° (3rd 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 1-min break between the first error clamp block and the reverse error clamp block. During this break, the experimenter informed participants that the cursor feedback would 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 >90° from the target location. These were removed from the analysis and constituted only eight trials out of a total set of 5,760 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 preprocessed.

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 whether the observed hand angle diverged from the hand angle during baseline reaches (*cycles 6–25*). Clusters were defined as epochs of two or more cycles in which *t* values exceeded a threshold of a *P* value <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) 1,000 times. A *P* value was 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 nonparametric 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 eight mini-blocks consisted 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 (Fig. 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; 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 (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 Fig. 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

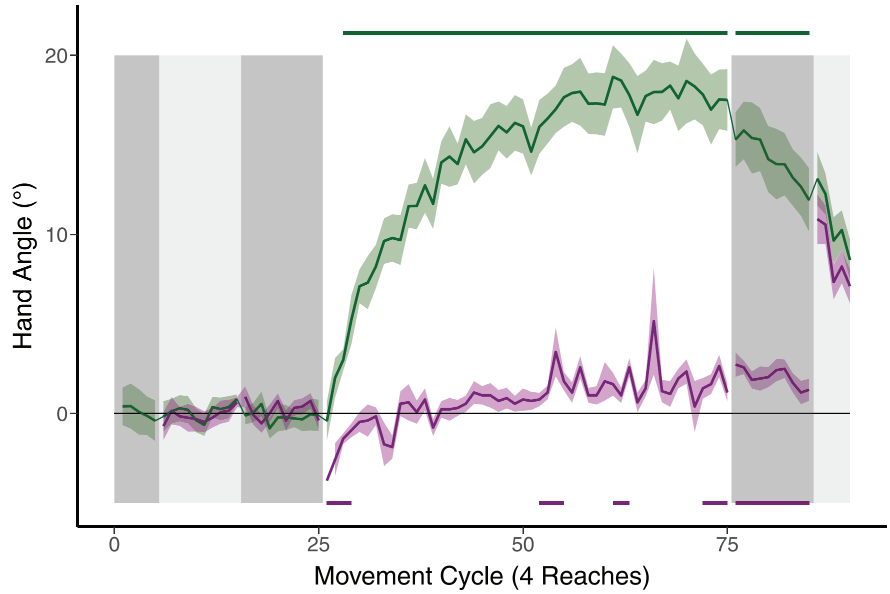

Fig. 2. Reaching (green) and hand position report (purple) functions for *experiment 1*. Target position is always at 0°. Vertical shading indicates feedback for each block (light gray, veridical; dark gray, no feedback; white, visual error clamp). Clusters in which hand report (purple; *bottom*) and hand angle (green; *top*) data are significantly different from baseline are denoted by the bars at the *bottom* and *top* of the graph, respectively. SE denoted by shaded region around each function.

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 >5° (a conservative cutoff), almost half of which were driven by one participant (9 out of 22 reports). Thus, the shift of perceived hand location toward 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.

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. Although 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 nonveridical 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 that 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 have resulted in a shift in the direction of the heading angle for the hand, eventually reaching a similar asymptotic value in the opposite direction. We could then examine whether the hand report data showed a similar reversal.

During the initial clamp block, hand angle again deviated in a direction opposite the clamp, the signature of adaptation (Fig. 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 (nonasymptotic) mean value of −11.5° (−25.0°, −2.5°). The deviation in the opposite direction of the clamp was significantly different from 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 Fig. 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

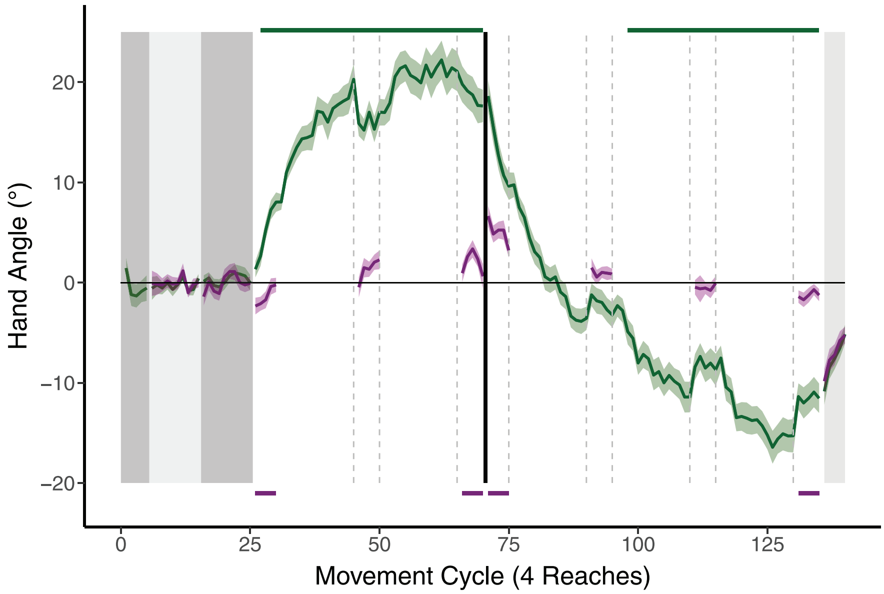

Fig. 3. Reaching (green) and hand position report (purple) functions for *experiment 2*. Note that hand reports were only obtained in an intermittent manner. Target position is always at 0°. Vertical shading indicates feedback for each block (light gray, veridical; dark gray, no feedback; white, visual 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 the 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. SE denoted by the shaded region around each function.

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 of the evolving change in actual hand position. Given that the hand reports were obtained intermittently, nonparametric 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°), $d_z = 0.075$]. 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 from 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 toward the visual error clamp and a gradual shift in the direction of adaptation that reached a peak of ~2°. We assume that 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 ($R_{Spearman} = 0.5$, $P < 0.001$; Fig. 4).

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 et al. 2010). Several lines of evidence highlight the implicit nature of adaptation. Retrospective queries assessing participants' phenomenological experience after learning suggest that the change in behavior is largely implicit (at least for rotations up to 30–45°). Perhaps most compelling is that 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 not accounted for when the participants are asked to report their intended movement direction before the reach (Taylor et al. 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

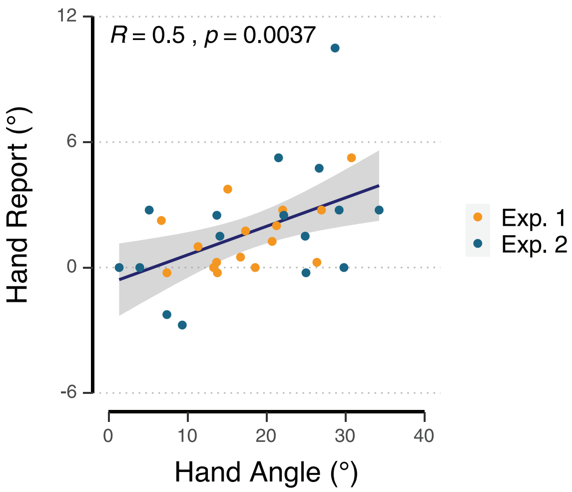

Fig. 4. Spearman correlation between hand angle and hand reports during late adaptation, pooling together data from *experiment 1* (*cycles 71–75*, yellow circles) and *experiment 2* (end of 1st clamp block; *cycles 66–70*, blue circles). Correlations are marginally significant if data from each experiment 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, whereas the gray shaded region corresponds to the 95% confidence interval.

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. Although 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 et al. 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 at 25–30°, it is likely that many participants would remain unaware 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 toward 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 toward 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° toward the visual feedback) and rapid onset with the proprioceptive shift reported in previous studies (Cressman and Henriques 2009, 2010; Ruttle et al. 2016; Salomonczyk et al. 2011). 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 ∼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 et al. 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 et al. 2020). That is, participants have a strong belief that their 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 their state but remains insensitive to the changes enacted by their brain to compensate for their fatigue.

ACKNOWLEDGMENTS

We thank Odeya Kagan and Janet Hwang for their assistance with data collection. We thank Guy Avraham for his astute comments on this article.

GRANTS

J.S.T was funded by a 2018 Florence P. Kendall Scholarship from the Foundation for Physical Therapy Research. This work was supported by grants NS092079 and NS116883 from the National Institutes of Health.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

J.S.T., D.P., and R.B.I. conceived and designed research; J.S.T. and D.P. performed experiments; J.S.T. and D.P. analyzed data; J.S.T., D.P., and R.B.I. interpreted results of experiments; J.S.T. and D.P. prepared figures; J.S.T. drafted manuscript; J.S.T., D.P., and R.B.I. edited and revised manuscript; J.S.T., D.P., and R.B.I. approved final version of manuscript.

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