Task Errors Do Not Induce Implicit Sensorimotor Learning

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ABSTRACT

Humans implicitly adjust their movements when challenged with perturbations that induce sensory prediction errors. Recent work suggests that failure to accomplish task goals could function as a gain on this prediction-error-driven adaptation or could independently trigger additional implicit mechanisms to bring about greater net learning. We aimed to distinguish between these possibilities using a reaching task wherein prediction errors were fixed at zero, but task success was modulated via changes in target location and size. We first observed that task failure caused changes in hand angle that showed classic signatures of implicit learning. Surprisingly however, these adjustments were eliminated when participants were explicitly instructed to ignore task errors. These results fail to support the idea that task errors independently induce implicit learning, and instead endorse the view that they provide a distinct signal to an intentional cognitive process that is responsive to verbal instruction.

INTRODUCTION

The sensorimotor system is continuously challenged with changes in the state of the body and the world. For instance, a golfer may have to tee off against a constant breeze, or a dancer may have to perform while wearing a heavier-than-usual costume. Understanding how we adapt our movements to such changes has been of tremendous interest in sensorimotor neuroscience. Laboratory tasks often simulate such conditions using various visual (Krakauer, 2009; Kumar et al., 2020; Martin et al., 1996; Morehead et al., 2017; Wang & Sainburg, 2005) or dynamic (Dizio and Lackner, 1995; Kumar et al., 2019; Sainburg et al., 1999; Shadmehr and Mussa-Ivaldi, 1994; Sing et al., 2009) perturbations that not only induce a discrepancy in the expected versus actual sensory feedback (sensory prediction error, SPE), but can also result in a failure to achieve the task goal (task error, TE). It is generally believed that SPEs are compensated via implicit updates to internal neural representations that define the relationship between movement commands and their sensory consequences. Findings that adaptation results in after-effects post-learning, is relatively similar for different SPE magnitudes (Kim et al., 2018; Wei and Körding, 2009), can be quite inflexible (Bond and Taylor, 2015) and is impervious to verbal instruction (Mazzoni and Krakauer, 2006; Morehead et al., 2017) provide support to this view.

In contrast, controversy exists about how TEs influence adaptation. One hypothesis is that TEs trigger intentional, deliberative re-aiming strategies (Day et al., 2016; McDougle et al., 2015; Taylor et al., 2014). Such strategy use promotes faster error reduction (McDougle et al., 2015) and can be combined with the slower implicit mechanisms to achieve higher levels of learning (Langsdorf et al., 2019). However, an alternate view has emerged from recent work that has examined how binary reward influences adaptive behavior (Kim et al., 2019; Leow et al., 2018; Van der Kooij et al., 2018). These studies suggest two possible effects. First, reward (task success, no TE) might attenuate or interfere with adaptation driven solely by the SPE. Alternatively, the absence of reward (TE present) could independently trigger a second implicit process that sums with SPE-mediated learning to produce higher net adaptation. Here we aimed to distinguish between these two possibilities using an unconventional paradigm in which we "clamped" SPEs to zero but manipulated TEs using target displacements.

RESULTS

Subjects performed point-to-point reaches on a digitizing tablet with the hand hidden from direct view using a mirror and display-screen system (Figure 1A). In experiment 1 (Figure 1B), subjects were randomly assigned to a "Miss" (TE present) or a "Hit" (no TE) group, with SPE fixed at zero for both groups. We predicted that if adaptation was exclusively SPE-driven, neither group would adapt. We found (Figure 2A) large changes in hand angle for the Miss compared to the Hit group during the learning block. While early learning (Figure 2B) was not different between the two groups (Hit mean±SE = 0.910±0.630, Miss mean±SE = 3.870±1.727, $t_{17.66} = -1.61$, $p = 0.125$, Cohen's *d* = -0.588), hand deviation of the Miss group was much larger at the end of learning (Figure 2C, Hit mean±SE = 5.822±2.079, Miss mean±SE = 24.480±3.211, $t_{23.99} = -4.878$, $p < 0.001$, Cohen's *d* = -1.781). Notably, it was not the case that the Hit group showed no changes in hand angle. A direct comparison of early and late learning within the Hit participants revealed a small but significant shift in mean hand angle ($t_{14} = -2.726$, $p = 0.016$, Cohen's *d* = -0.704), but clearly, compared to the

Miss group, this learning was strongly attenuated. Relatedly, larger after-effects (Figure 2C, $t_{27.98} = -4.011$, $p < 0.001$, Cohen's d = -1.465) were seen in the Miss group (mean±SE = 13.978±1.740); after-effects for the Hit group were quite small, but non zero (mean±SE = 3.960±1.792, 95% CI = [0.117, 7.803]). Interestingly, as Figure 2A indicates, the net change in hand angle for the Miss group was greater than the magnitude of the TE itself (10-degrees). This observation is consistent with what has been observed for small SPEs (Kim et al., 2018), and along with the robust after-effects, suggests that this learning was implicit.

A key signature of implicit adaptation is that it is impervious to verbal instruction (Mazzoni and Krakauer, 2006; Morehead et al., 2017). We therefore hypothesized that if the learning seen in experiment 1 was truly implicit, it would occur even when participants are instructed to ignore the TE. In experiment 2, we recruited two groups of subjects who underwent learning exactly as the Miss group of experiment 1, but were told to ignore the (10- or 20-degree) TE and reach to the original target location. Surprisingly, we now found (Figure 3A) that there was no change in hand angle over the learning block for either group. The deviation in hand angle during early learning (Figure 3B) remained close to zero for the 10-degree jump (mean±SE = -0.154±0.29, 95% CI = [-0.777, 0.468]) as well as the 20-degree jump (mean±SE = 0.687±0.378, 95% CI = [-0.123, 1.498]). This was also the case towards the end of the learning block (10-degree shift: mean±SE = -1.843±0.887, 95% CI = [-3.747, 0.06], 20-degree shift: mean±SE = -1.182±0.863, 95% CI = [-3.033, 0.67]). After-effects were also absent both groups (10-degree shift: mean±SE = -0.951±1.183, 95% CI = [-3.488, 1.585], 20-degree shift: mean±SE = -0.648±0.708, 95% CI = [-2.167, 0.871]). Thus, when asked to ignore the

TE, subjects showed no adaptive change in reach behavior regardless of the magnitude of the TE; this is inconsistent with what would be expected from an implicit learning process.

DISCUSSION

We probed how failure or success in achieving task goals influences adaptive motor behavior. On the face of it, the adaptive response to target misses in experiment 1 was implicit and mediated by the TE since the SPE was clamped to zero. But, if this were true, it should not have been abolished by the instruction to ignore the TE. How do we reconcile these contrasting positions? We propose the intriguing possibility that learning in the Miss group was driven not by a TE, but rather by a "hidden" SPE caused by the mismatch between the subjects' expectation that the feedback cursor would go with the hand as they reached to the displaced target, and its actual motion in the clamped direction towards the original target. Thus, learning that *appeared* to be due to a TE, was driven, in all likelihood, by an SPE that the task conditions created. Lending support to this idea is firstly the result the net change in hand angle was much larger than the TE magnitude and secondly the finding that adaptation occurred despite the instruction to ignore cursor feedback. Both these effects are known to occur for SPE-mediated adaptation (Kim et al., 2019, 2018; Morehead et al., 2017). Furthermore, in experiment 2, task conditions likely eliminated the covert SPE since subjects moved to the original target location (as instructed) with cursor motion clamped in the same direction. Since the SPE was no longer present, subjects did not adapt despite the presence of the TE. This result, that the sensorimotor system can tolerate (or ignore) TEs but adapts when an SPE is present, is consistent classic work by Mazzoni and

Krakauer (2006), as well as other findings in healthy individuals (Tseng et al., 2007) and patients with focal, right frontal lesions (Mutha et al., 2011a). Tellingly, Wang et al. (2019) have suggested that the SPE dominance may be so strong that TEs may have negligible influence at least in canonical adaptation paradigms.

If the SPE drives the implicit change, how does the TE contribute? Our intervention requiring subjects to ignore the TE and the subsequent yoking of the behavior to this instruction, lends credence to the idea that TEs provide a distinct error signal that can potentially set in motion an intentional mechanism that causes people to re-aim their hand movement (Day et al., 2016; McDougle et al., 2015; Taylor et al., 2014). Thus, when subjects are expected to “respond” to the TE, they may deliberatively change their movement aim to cancel it, but when asked to ignore it, they turn off this strategy. Relatedly, aiming strategies might also be disengaged when task conditions do not induce a TE at all and movements are always successful (or rewarded). Net adaptation would then be determined only by the implicit process; this could explain recent findings that provided the impetus for the current study (Kim et al., 2019; Leow et al., 2018; Van der Kooij et al., 2018). Such flexibility is indeed a hallmark of strategy use, but not implicit learning (Bond and Taylor, 2015). Strategies may include mental rotation of the original movement plan by an angle matching the TE (Fernandez-Ruiz et al., 2011; McDougle and Taylor, 2019) or even goal-directed control akin to model-based reinforcement learning. These intentional processes could enable a rapid reduction in error (McDougle et al., 2015), and additively combine with the slower SPE-mediated implicit changes to produce the net adaptive change. Indeed, it has been shown that adaptation, which otherwise remains incomplete (Hinder et al., 2010; Shmuelof et al., 2012; Vaswani et al., 2015), becomes more complete when task conditions promote strategy use (Langsdorf et al., 2019).

The distinction between SPE- and TE-sensitive mechanisms suggests that they might also be neurally separable. While SPE-based learning depends on the cerebellum (Galea et al., 2011; Martin et al., 1996; Morehead et al., 2017; Tseng et al., 2007) and parietal cortex (Kumar et al., 2020; Mutha et al., 2011a, 2011b, 2017), the presence of a TE is known to activate reward-sensitive cortico-striatal pathways (Diedrichsen et al., 2005; Inoue et al., 2016). Failure to obtain reward could trigger re-aiming via mental rotation or other processes dependent on M1 and premotor cortex (Georgopoulos & Massey, 1987; Georgopoulos et al., 1989; Kosslyn et al., 1998; Tomasino et al., 2005). Indeed, changes in these regions following learning (Mandelblat-Cerf et al., 2011; Paz et al., 2003; Perich et al., 2018) may partially reflect changes in motor plans driven by such processes. Future work could probe the interactions between these two systems, which, neuroanatomically could be sustained by reciprocal connections between the basal ganglia and the cerebellum (Bostan and Strick, 2018).

MATERIALS AND METHODS

Participants

We recruited 60 healthy, right-handed adults (41 males, 19 females, age range: 18-40) for the study. The Edinburgh handedness inventory (Oldfield, 1971) was used to establish right-handedness. None of the participants reported any neurological, orthopaedic or cognitive impairments. All subjects gave written informed consent and were monetarily compensated for their time. The study was approved by the Institute Ethics Committee of the Indian Institute of Technology Gandhinagar.

Apparatus

The experimental setup consisted of a virtual reality system wherein participants sat facing a digitizing tablet and used a stylus to make hand movements on it (Figure 1A). A high-definition display was mounted horizontally above the tablet and was used to show circular start positions and targets for the reach, as well as a feedback cursor that would typically indicate hand (stylus) location on the tablet. Participants looked into a mirror which was suspended between the display and the tablet, and which reflected the display screen. The mirror also functioned to block direct vision of the arm. This arrangement enabled us to dissociate motion of the feedback cursor from that of the hand. For instance, cursor feedback could be veridical with the hand, “clamped” in certain directions independent of hand movement direction, or eliminated altogether.

Task Procedure and Experimental Design

The task involved making centre-out reaching movements from a fixed start circle (0.9 cm diameter) to a target. To initiate a trial, participants first moved their hand (cursor) into the start circle. After 500 ms, the reach target (0.98 cm diameter) was displayed along with a beep, which indicated to subjects that they should begin moving. Targets were presented at a distance of 10 cm and could appear at one of four locations arranged radially around a virtual circle in 90-degree increments (0, 90, 180, 270). The order of target appearance was pseudo-random; a target appeared in one of the four locations only once over four consecutive trials. This order was held constant for all participants. Cursor feedback, whenever provided, was shown only for a distance of 10 cm at which point the cursor “froze” and stayed in place even though the hand could continue moving.

Experiment 1

After familiarization with the setup and a few practice trials (not analyzed), subjects made "baseline" reaches in two blocks. In the first block (20 trials), no cursor feedback was shown as subjects moved between the start position and the target. In the second baseline block (20 trials), the feedback cursor was shown veridical with the hand. Following baseline movements, subjects were exposed to a "learning" block (240 trials) during which the motion of the cursor was "clamped" in the direction of the target. In other words, in this block, the cursor always followed a direct, straight path to the target regardless of the direction of hand motion. Subjects were informed and made to understand that the cursor feedback would be fixed and would not depend on their hand movements. They were also explicitly told to ignore this feedback and move towards the target on the screen. A reminder about this was provided at the halfway point of the learning block. Post-learning, subjects performed a set of 20 trials without any visual feedback to test for potential after-effects, and a final block of 20 trials in which veridical cursor feedback was again provided. These two "washout" blocks were thus similar to the two baseline blocks.

The participants of experiment 1 were randomly divided into two groups, "Miss" or "Hit" (n=15 each). For the Miss group, on each trial of the learning block, the target was "jumped" by 10-degrees in the counter-clockwise direction as the hand crossed the mid-way point to the target. Essentially, the original target was extinguished and a new target was displayed at the 10, 100, 190 and 280 degree locations for the 0, 90, 180 and 270 degree targets respectively. Since the cursor was clamped to go towards the original target, this "jump" resulted in the cursor missing the (new) target, creating a task error. For the Hit group, identical target jumps were implemented but the size (diameter) of the new target was simultaneously increased from the original 0.98 cm to 4.6 cm. This was done to ensure that the clamped cursor would still hit the new target even though its location had been shifted. The hit was not exactly in the center of the displaced target, but close to it.

Experiment 2

The results of our first experiment indicated that subjects in the Miss group implicitly changed their hand reach direction. We hypothesized that if this learning was truly implicit, it would be unresponsive to a verbal instruction to ignore the target jump. To test this idea, we recruited two additional groups of subjects (n=15 each), who experienced target jumps of two different amplitudes (10- or 20-degrees). All subjects were presented with the exact same experimental protocol as the Miss group of experiment 1. Critically however, both groups of subjects were now also explicitly instructed to ignore the change in target location. As in experiment 1, subjects were reminded of this halfway into the learning block as well.

Data Analysis and Statistics

Hand position data (X-Y coordinates) were filtered using a low-pass Butterworth filter with 10-Hz cutoff frequency. Velocity values were obtained by differentiating the position data. The primary dependent variable was the deviation in hand direction relative to original (not jumped) target direction. This was computed as the angle between the line connecting the start position to the original target, and the line connecting the start position to the hand position at peak movement velocity. Trials in which participants did not initiate a movement or lifted the stylus off the tablet mid-trial leading to loss of data were marked as “bad trials” and excluded from the analysis. Additionally, trials in which hand deviation was more than 85˚ were also removed. Collectively, across the 60 participants, 2.1% of the trials were excluded.

We then calculated baseline directional biases, defined as the mean hand deviation across all baseline trials. These biases were subtracted from the trial-wise angular deviation data. Learning was quantified using the trial-by-trial values of the baseline subtracted hand deviation over the learning block. For each subject, early learning was calculated as the mean deviation over the first 10 learning trials while late learning was characterized by the mean deviation over the last 10 learning trials. Similarly, after-effect magnitude was quantified as the mean deviation over the first 10 trials of the post-learning no-feedback block.

Differences in hand deviation between the Hit and Miss groups of experiment 1 during early and late learning as well as early after-effect stages were compared using Welch’s t-tests after checking for normality with Shapiro-Wilk tests. Paired t-tests were used for assessing changes in hand deviation across different time points within a group. Significance levels were set at 0.05. Cohen’s *d* was used for estimating the effect size of the differences. For experiment 2, we used the 95% confidence interval to probe for significant deviation in hand angle during early and late learning as well as the early after-effect stages for both the 10-degree and 20-degree jump groups.

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FIGURE LEGEND

Figure 1: Experimental setup and Task. (a) Subjects performed reaching movements on a digitizing tablet using a handheld stylus while looking into a mirror placed between the tablet and a horizontally mounted display screen. Start positions, targets, and a feedback cursor was displayed on the screen, which were reflected in the mirror. **(b)** On the learning trials of experiment 1, the reach target was "jumped" by 10-degrees counterclockwise while cursor motion was always clamped in the direction of the original target (SPE = 0). For participants in the Miss group, this arrangement resulted in a TE since the cursor failed to strike the displaced target. For participants in the Hit group, target size was increased along with the jump, which caused the clamped cursor to hit the new target despite the shift in its location; this resulted in a condition where both SPEs and TEs were eliminated. In experiment 2, participants were exposed to conditions similar to the Miss group, but were additionally explicitly instructed to ignore the (10- or 20-degree) target shift and move towards the original target location.

Figure 2: **Pattern of hand angle changes in experiment 1. (a)** Group averaged hand angle deviation (relative to the original target direction) across trials of different experimental blocks. During learning, greater net change was seen for the Miss compared to the Hit group; learning in the Hit group was strongly attenuated. Shaded regions denote SEM. **(b)** On average, early learning was not different between the groups, but the Miss group showed significantly greater hand deviation at **(c)** the end of learning and also demonstrated **(d)** larger after-effects. Interestingly, although the target jump was only 10-degrees, the net change in hand angle for the Miss group was ~2.5 times this magnitude. Dots represent individual participants.

Figure 3: **Pattern of hand angle changes in experiment 2 wherein participants were explicitly instructed to ignore the target jump. (a)** Group averaged hand angle deviation across trials of different blocks. No major deviation was seen in the hand angle (relative to the original target location) across trials. Shaded regions denote SEM. **(b)** Average hand angle deviation remained close to zero during early as well as late learning stages, and after-effects were also absent in both the 10-degree and 20-degree target jump groups. Thus, learning was generally suppressed when participants were instructed to ignore the target-jump-induced task error. Dots represent individual participants.

FIGURE 1

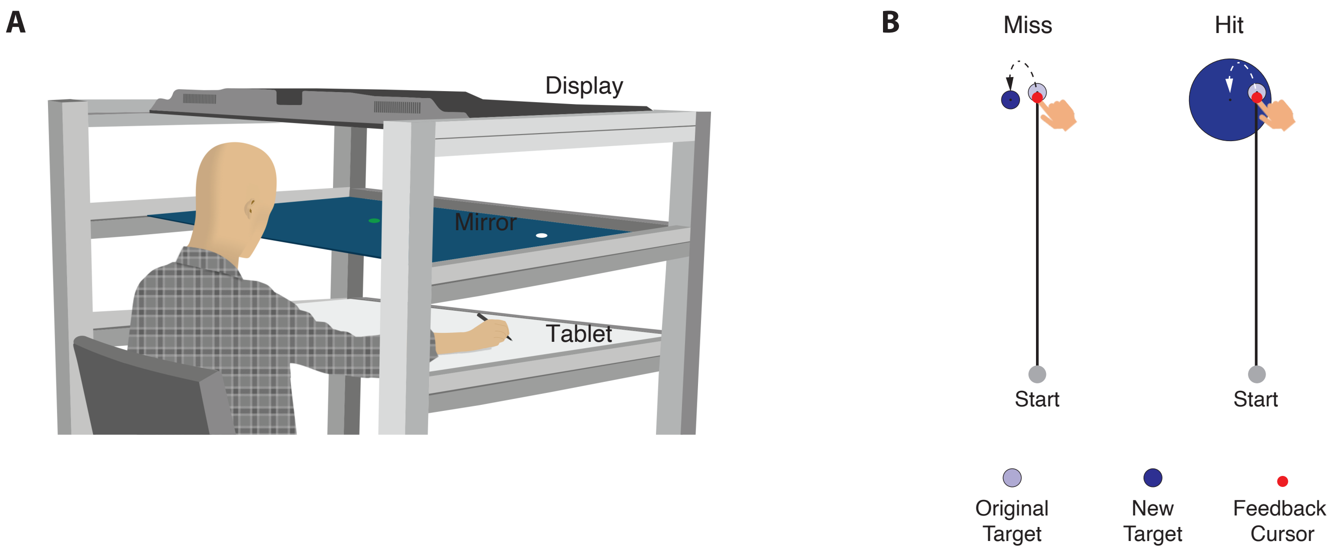

A
Display
Mirror
Tablet
B
Miss
Hit
Start
Start
Original Target
New Target
Feedback Cursor

FIGURE 2

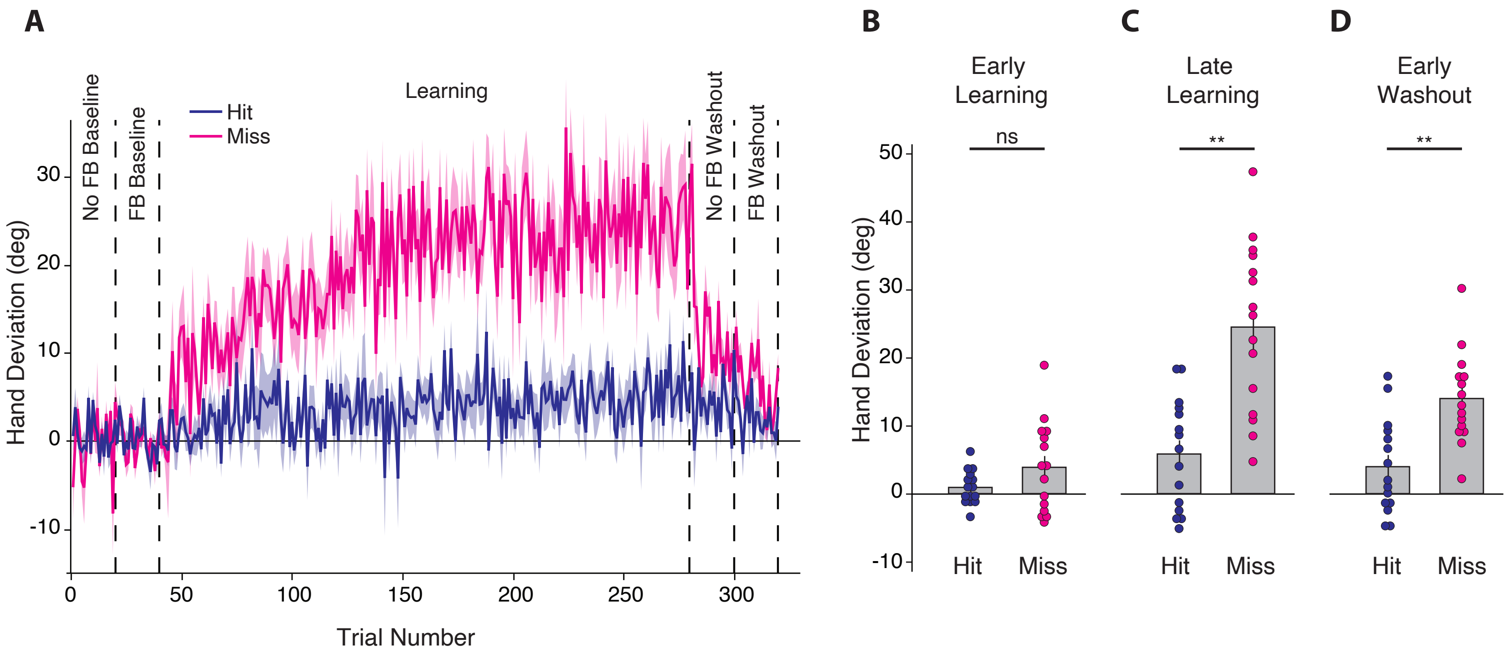
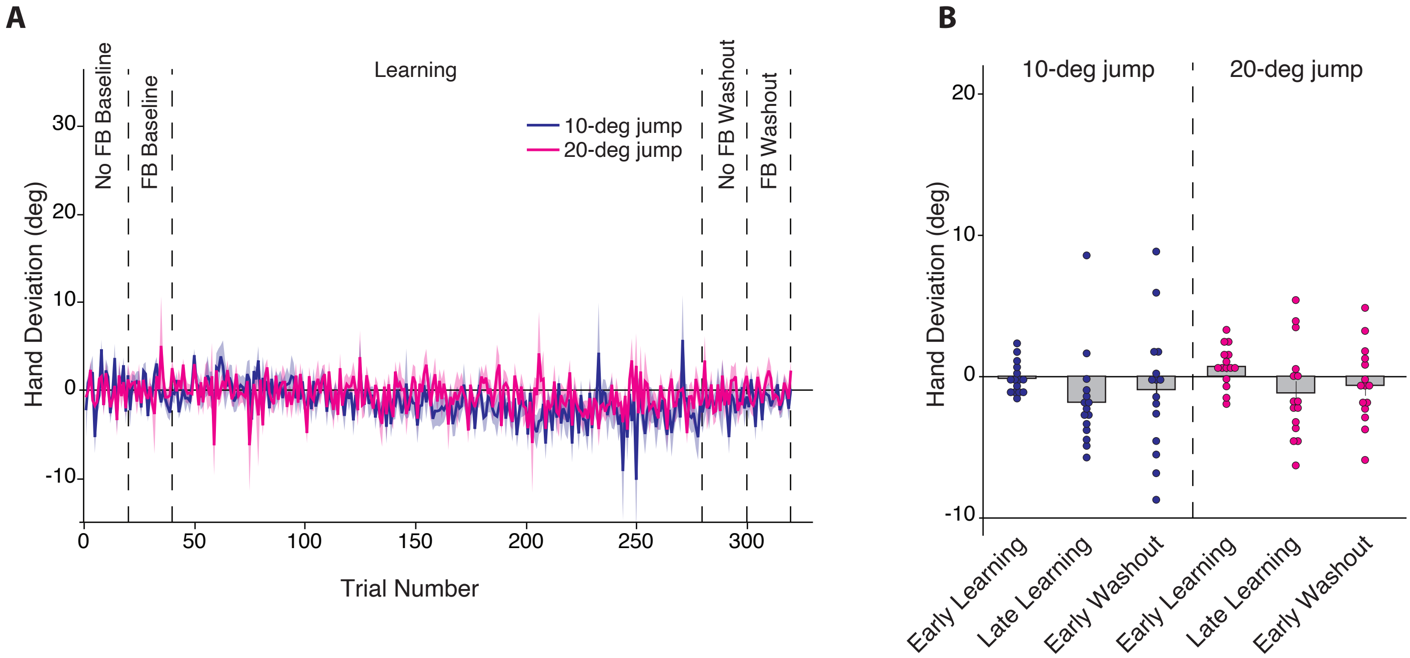

A
B
C
D
No FB Baseline
FB Baseline
Learning
No FB Washout
FB Washout
Hit
Miss
Hand Deviation (deg)
Trial Number
Early Learning
Late Learning
Early Washout
ns
**
**

FIGURE 3


A
No FB Baseline
FB Baseline
Learning
No FB Washout
FB Washout
10-deg jump
20-deg jump
Hand Deviation (deg)
Trial Number
B
10-deg jump
20-deg jump
Hand Deviation (deg)
Early Learning
Late Learning
Early Washout
Early Learning
Late Learning
Early Washout