

RESEARCH ARTICLE

Control of Movement

Minimal impact of chronic proprioceptive loss on implicit sensorimotor adaptation and perceived movement outcome

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Abstract

Implicit sensorimotor adaptation keeps our movements well calibrated amid changes in the body and environment. We have recently postulated that implicit adaptation is driven by a perceptual error: the difference between the desired and perceived movement outcome. According to this perceptual realignment model, implicit adaptation ceases when the perceived movement outcome—a multimodal percept determined by a prior belief conveying the intended action, the motor command, and feedback from proprioception and vision—is aligned with the desired movement outcome. Here, we examined the role of proprioception in implicit motor adaptation and perceived movement outcome by examining individuals who experience deafferentation (i.e., individuals with impaired proprioception and touch). We used a modified visuomotor rotation task designed to isolate implicit adaptation and probe perceived movement outcomes throughout the experiment. Surprisingly, both implicit adaptation and perceived movement outcome were minimally impacted by chronic deafferentation, posing a challenge to the perceptual realignment model of implicit adaptation.

NEW & NOTEWORTHY We tested six individuals with chronic somatosensory deafferentation on a novel task that isolates implicit sensorimotor adaptation and probes perceived movement outcome. Strikingly, both implicit motor adaptation and perceptual movement outcome were not significantly impacted by chronic deafferentation, posing a challenge for theoretical models of adaptation that involve proprioception.

implicit recalibration; motor adaptation; motor learning; proprioception; visuomotor rotation

INTRODUCTION

Multiple learning processes operate to ensure that motor performance remains successful in the face of changes in the environment and body (1–3). For example, if a tennis ball is

consistently perturbed by the wind, the player can explicitly and rapidly adjust their swing to compensate. This perturbation will also engage an automatic, implicit adaptation process that uses the error information to recalibrate the sensorimotor system (4).

We have recently postulated that implicit adaptation is driven by a perceived movement error, the difference between the desired and perceived movement outcome (5, 6). According to this perceptual realignment model,¹ the perceived movement outcome is a multimodal percept. Feedback can be provided from visual and proprioceptive receptors (i.e., muscle

¹In the original exposition of this model, we used the term “proprioceptive realignment.” However, recognizing that perceived movement outcome is influenced by feedback from vision and proprioception, the prior expectation conveying the intended action, and the efferent motor command (7–10)—a point made salient by Zhang et al. (5)—we now adopt the phrase “perceptual realignment” to better capture this idea.



spindles, Golgi tendons, skin stretch). But the perceived movement outcome is also influenced by predictive signals that include sensory predictions derived from an efference copy of the motor command (11–14) and a prior belief concerning the expected outcome of the forthcoming action (15).

In an upper limb reaching task, perturbing the relationship between the participant's visual cursor and movement effector will shift the perceived movement outcome toward the perturbed visual cursor and, thus, away from the actual effector as well as away from the target. This perceived movement error would drive movements of the hand/arm in the opposite direction to the visual perturbation (implicit adaptation). When the perceived error is nullified, that is, when the perceived outcome is aligned with the desired outcome, implicit adaptation will cease (for a review, see Ref. 6).

Individuals lacking proprioceptive and tactile inputs from the upper limb, a condition known as somatosensory deafferentation, provide a unique opportunity to understand the role of proprioception in implicit motor adaptation. Deafferentation, which can result from either a congenital disorder or a neurological insult, is rare (16–23). Previous case studies have shown that motor adaptation is minimally impacted in deafferented adults (20, 21, 24–27). However, the tasks used in these studies did not isolate implicit adaptation, meaning learning performance could also be influenced by explicit, strategic processes (3, 25). This makes it challenging to determine whether implicit adaptation is reduced, minimally impacted, or even enhanced compared with controls. Moreover, the impact of proprioceptive loss on the perceived movement outcome during implicit adaptation is unknown.

To fill this gap, we tested a cohort of deafferented individuals on a clamped visuomotor rotation task that isolates implicit adaptation and probes perceived movement outcome (28, 29) (Fig. 1A). In this task, participants reach to a visual target and the visual feedback (i.e., a white cursor on the computer screen) follows a fixed trajectory defined relative to the target. Thus, unlike standard perturbation methods, the direction of the visual feedback is not contingent on the participant's movement direction. Participants are fully informed of this manipulation and instructed to always reach directly to the target while ignoring the visual feedback. Despite these explicit instructions, the visual perturbation between the position of the target and the cursor elicits an implicit adaptive response in healthy participants, causing a gradual trial-by-trial change in movement direction away from the target and in the opposite direction to the visual cursor. These motor adjustments are not the result of explicit reaiming; indeed, participants are oblivious to the change in their movement (28). Furthermore, participants were periodically asked to report their perceived movement outcome using a wheel of numbers (Fig. 1B), providing a measure of their perceived movement error—the distance between the perceived movement outcome and the visual target.

Based on the perceptual realignment model, we tested two core predictions. First, there should be a heightened perceived error in the deafferented group compared with that of the control group. With the loss of proprioception, we predicted the deafferented group would rely heavily on visual feedback of the cursor to determine perceived movement

outcome and thus show a heightened perceived movement error. Consequently, an increase in the perceived movement error in the deafferented group would result in heightened implicit adaptation, requiring a larger change in movement angle to offset the larger error.

METHODS

Ethics Statement

The study protocol was approved by the UC Berkeley's Institutional Review Board. All participants gave written informed consent. Participation in the study was in exchange for monetary compensation.

Participants

We recruited deafferented participants who, despite their severe upper-limb sensory loss, could perform a simple reaching task. Given the rarity of this condition and issues with functional mobility, we used an online approach to test six chronic, deafferented participants spread across four countries (Tables 1 and 2). This sample is larger and more etiologically diverse than those recruited in prior studies. All deafferented participants reported having corrected or uncorrected vision greater than 19/20.

Although there are no definitive standards for clinically evaluating proprioception, we reviewed the medical reports for each deafferented participant. For all the patients, the reports indicated loss of somatosensory reflexes and proprioceptive loss in the hand and in the forearm. Abnormalities were noted on proprioceptive position matching tasks (wrist, elbow, and shoulder), tactile discrimination tasks, and vibration perception. The reports noted severe ataxia while performing pegboard tests and when writing with their dominant hand. All deafferented participants had severe gait impairments and, except for CD, all required support for their daily needs (walker, wheelchair, or a caretaker).

In the next two paragraphs, we detail the specific clinical etiologies for each participant. Note that all the participants with acquired deafferentation have previously participated in other studies. For further details on their clinical presentations, we refer readers to the cited references. The three participants with congenital deafferentation have impaired proprioceptive and tactile perception, resulting in severe motor ataxia: CM and SB have an autosomal recessive mutation in the mechanoreceptor *PIEZO2* gene (19), while CD has an inherited mutation in the mechanoreceptor *ASIC3* gene (30).

The three other participants acquired deafferentation following an acute neurological episode. IW suffered sensory neuropathy at age 19 yr from an autoimmune response to a viral infection, resulting in severe proprioceptive and tactile impairment below the neck (18, 31). WL experienced a bout of polyradiculitis at age 31, leading to severe proprioceptive and tactile impairments below the neck (21, 32). DC has severe proprioceptive impairment in the right upper limb subsequent to surgical resection of a vascular tumor at age 38 near the right medulla oblongata (22, 33).

A total of 60 control participants were recruited to closely match each of the deafferented participants in terms of age, sex, handedness, and device used in the experiment (Table 2). Previous studies on deafferented participants typically

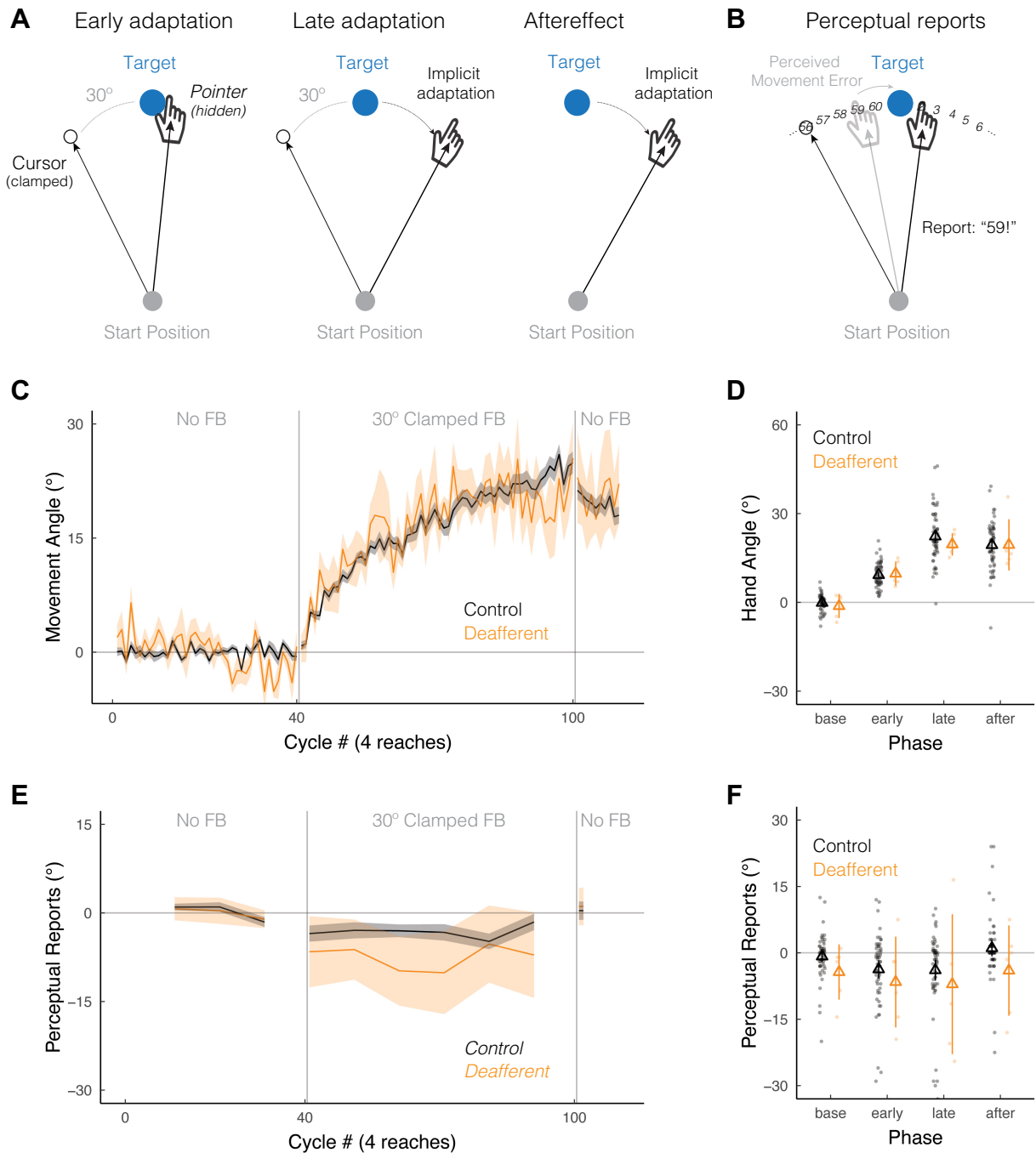


Figure 1. Minimal impact of proprioceptive loss on implicit motor adaptation and perceived movement outcome. **A:** schematic of the visual clamped feedback task. After baseline trials without visual cursor feedback (cycles 1–40), participants were exposed to 240 trials with clamped visual feedback (cycles 41–100) in which the cursor (white circle) followed a fixed trajectory, rotated 30° counterclockwise relative to the target and irrespective of the participant’s movement. Participants were instructed to always move their pointer (hidden or visible) directly to the target (blue circle) and ignore the visual clamped cursor feedback. The pointer represents the veridical representation of the fingertip position in trackpad or mouse coordinates on the computer screen. *Left, middle, and right:* schematics of pointer and cursor positions during the early (cycles 41–60), late (cycles 81–100), and aftereffect (cycles 101–110) phases of adaptation, respectively. **B:** every 10th cycle, participants reported their perceived movement outcome. On these trials, a number wheel would appear on the screen as soon as the amplitude of the movement reached the target distance, cueing participants for a report (top). The numbers (“1” to “60”) increased incrementally in the clockwise direction (spaced at 6° intervals around the circle), with the number “1” positioned at the target location. Participants used their keyboard to type the number closest to their perceived movement outcome when reaching the target distance. Mean time courses of movement angle (C) and perceptual reports (E) for Control (black; $n = 60$) and Deafferented groups (orange; $n = 6$). Shaded areas represent standard error. Both measures are presented relative to the target (0°); negative and positive values denote movements/reports toward or away from the cursor, respectively. One cycle consisted of four movements, one to each of the four possible target locations. Summary of implicit adaptation (D) and perceptual report data (F) over baseline, early, late, and aftereffect phases. Error bars denote 95% confidence intervals. Triangle denotes the mean for each group. Dots denote individuals.

Table 1. Deafferented participant demographics

Name	Etiology	Age	Years Since		Sex	Handedness
			Onset			
CD	Congenital	22	22		F	R
CM	Congenital	46	46		M	R
SB	Congenital	34	34		F	R
DC	Acquired	54	16		F	R
IW	Acquired	70	51		M	L
WL	Acquired	53	22		F	L

Participants were identified as either male (M) or female (F), right-handed (R) or left-handed (L).

recruit five controls per patient (21, 34). To ensure a more conservative and robust sample, we opted to double this number to 10 in our study. Control participants were recruited via Prolific, an online crowdsourcing platform that connects researchers with willing participants worldwide. This platform allows us to find control participants closely matched to deafferented participants in terms of age, sex, handedness, and preferred device used (mouse or trackpad) in daily life. All control participants reported to have corrected or uncorrected 20/20 vision.

The deafferented participants completed the task during a live video session, with the experimenter available to provide instructions and monitor performance. The control participants completed the task autonomously, accessing the website at their convenience.

Apparatus

Participants used their own computer to access a dynamic webpage (HTML, JavaScript, and CSS) hosted on Google Firebase (35). The task progression was controlled by JavaScript code running locally in the participant's web browser. The participant's screen size was automatically detected, and this information was used to scale the size and position of the stimuli. There was no significant difference in screen size between groups [height: $t(9) = 0.4$, $P = 0.71$, $D = 0.1$; width: $t(10) = 1.8$, $P = 0.10$, $D = 0.6$]. For ease of exposition, the parameters below are based on the average screen size (width \times height: 1,455 \times 831 pixels).

We note that, unlike our laboratory-based setup in which we occlude vision of the reaching hand, this was not possible with the online testing protocol. That being said, we have found that measures of implicit adaptation are similar between in-person and online settings (35).

Procedure

Participants used a trackpad or a mouse to move a computer cursor, with the device based on their personal preference in daily life. The center-out movements were performed with their dominant hand, starting from the center of the workspace and attempting to slice through the visual target. A

white annulus (0.5 cm in diameter) indicated the center position, a blue circle indicated the target location (0.5 cm in diameter), and the cursor was a white dot (0.5 cm in diameter). There were four possible target locations equally spaced around the workspace (45°, 135°, 225°, 315° where 0° corresponds to the rightward direction). On each trial, the target location was selected in a pseudo-randomized manner, with each target appearing once every cycle of four trials. The radial distance of the target from the start location was 8 cm on the visual display. The physical movement distance was likely between 6 and 10 cm (set to fit within the perimeter of the trackpad/tabletop), determined by the sensitivity (gain) setting of the participants' device.

Before starting the experiment, participants watched an instructional video that provided an overview of the procedure. They were instructed to proceed only if they understood the instructions and to rewatch the video if they did not (https://www.youtube.com/watch?v=to8EvqKmsO0&ab_channel=JonathanTsay).

At the beginning of each trial, the cursor appeared at a random position within 1 cm of the center of the screen. As such, the actual starting position varied subtly from trial to trial. The participant initiated the trial by moving the cursor to the center start location. After maintaining the cursor in the start position for 500 ms, the target appeared. Participants were instructed to move rapidly, attempting to "slice" through the target. There were three types of feedback cursor conditions during the experiment: no visual feedback, veridical visual feedback, and clamped visual feedback. During no-feedback trials, the cursor was extinguished as soon as the movement left the start annulus and remained off for the entire movement. During veridical feedback trials, the movement direction of the cursor was veridical with respect to the participants' movement direction. The veridical cursor was extinguished when the computer pointer (i.e., the veridical representation of the fingertip position in trackpad or mouse coordinates on the computer screen) crossed the radial target distance of 8 cm. Veridical feedback trials were only used at the beginning of the experiment to familiarize the participant with the task. During clamped feedback trials (Fig. 1A), the cursor moved at a 30° angular offset relative to the position of the target, counterclockwise and irrespective of the participant's actual movement direction—a manipulation used to isolate implicit adaptation (28, 29). The clamped cursor was extinguished when the movement distance exceeded the radial target distance of 8 cm.

Every 10th cycle, participants were asked to report their perceived movement outcome for four consecutive trials (i.e., one report per target location). There were a total of 40 "perceptual report" trials over the course of the experiment. On perceptual report trials, a number wheel appeared on the screen as soon as the clamped cursor reached the target

Table 2. Deafferented and age, sex, handedness, and device-matched control participants

Group	<i>n</i>	Age	Sex	Handedness	Device Used
Deafferented	6	46.3 (16.7)	2 M, 4 F	4 R, 2 L	1 Mouse (SB), 5 Trackpad
Control	60	45.1 (14.9)	20 M, 40 F	45 R, 15 L	16 Mouse, 44 Trackpad

Participants used either a mouse or trackpad to complete the experiment. The two groups were well matched on multiple dimensions [Age: $t(6) = 0.2$, $P = 0.86$, $D = 0.1$; Sex (M: male or F: female): $\chi^2(1,66) = 0$, $P = 1$; Handedness (R: right-handed or L: left-handed): $\chi^2(1,66) = 0.2$, $P = 0.66$; Device used for experiment: $\chi^2(1,66) = 0.3$, $P = 0.59$].

amplitude, cueing the participant for a report. The numbers (“1” to “60”) increased incrementally in the clockwise direction (spaced at 6° intervals around the circle), with the number “1” positioned at the target location. With their nondominant hand, the participant used the keyboard to report the number closest to their perceived movement position. Following the report, the white cursor appeared at a random position within 1 cm of the center start position. The participant moved the cursor to the start position to initiate the next trial.

The main task consisted of 110 cycles (four movements per cycle, 440 trials total) distributed across three main blocks of cycles/trials: A no-feedback block (40 cycles; 160 trials to assess baseline performance), clamped feedback block (60 cycles; 240 trials to assess adaptation), and a no-feedback block (10 cycles; 40 trials to assess aftereffects). Prior to the clamped feedback block, the following instructions were provided: “The white cursor will no longer be under your control. Please ignore the white cursor and continue to aim directly towards the target.”

To clarify the invariant nature of the clamped feedback, eight demonstration trials were provided before the first clamped perturbation block. On all eight trials, the target appeared straight ahead (90° position), and the participant was told to move to the left, to the right, and backward. On all these demonstration trials, the cursor moved in a straight line, 90° offset from the target. In this way, the participant could see that the spatial trajectory of the cursor was unrelated to their own movement direction.

To verify that the participants understood the clamped visual feedback manipulation task, we included an instruction check after eight demonstration trials in the adaptation block. The following sentence was presented on the screen: “Identify the correct statement. Press ‘a’: I will aim away from the target and ignore the white dot. Press ‘b’: I will aim directly towards the target location and ignore the white dot.” The experiment only progressed if participants pressed the “b” key. Indeed, all participants understood the instructions and pressed “b” to proceed.

Data Analysis

The main dependent variable for measuring adaptation was movement angle, defined as the angle of the computer pointer relative to the target when movement amplitude reached 8 cm from the start position. Note that the computer pointer is the veridical representation of the fingertip position in trackpad or mouse coordinates on the computer screen. This measure defines the angular difference between the target location and movement direction. Movement angles across different perturbation directions (clockwise and counterclockwise) were flipped such that negative and positive values always signified changes in movement angle toward and away from the perturbation, respectively. Recall that we asked participants to “slice through the visual target” and refrain from making online feedback corrections to isolate feedforward processes. Pilot work using our web-based platform indicated that movement trajectories were generally fast and straight, without evidence of online feedback corrections.

We defined four phases of adaptation: baseline, early adaptation, late adaptation, and aftereffect. Baseline performance was operationalized as the mean movement angle over the no-feedback baseline block (*cycles 1–40*), providing a measure

of stable baseline performance. Early adaptation was operationalized as the mean movement angle over the first 20 cycles of the clamped visual feedback block (*cycles 41–60*), capturing the steepest portion of the learning curve. Late adaptation was defined as the mean movement angle over the last 20 cycles of the clamped visual feedback block (*cycles 81–100*), representing the stable asymptotic phase of the learning curve. The aftereffect was operationalized as the mean movement angle over all 10 cycles of the no-feedback aftereffect block (*cycles 101–110*).

Outlier responses were defined as trials in which the movement angle was greater than 90° from the target or deviated more than three standard deviations from a trendline constructed with a moving 5-trial window. Outlier trials were excluded from further analysis since behavior on these trials could reflect anticipatory movements to the wrong target or attentional lapses (average excluded movement trials: Control group = $1.3 \pm 0.2\%$; Deafferented group = $1.1 \pm 0.3\%$).

The perceptual reports provide the dependent variable for measuring the perceived movement outcome. These data were converted into angular values, although we note that the perceptual reports involve categorical data (numbers spaced at 6° intervals), whereas in angular form they suggest a continuous variable. Outlier responses were removed in the exact same manner as the movement angle data (average excluded report trials: Control group = $1.8 \pm 1.0\%$; Deafferented group = $0.4 \pm 0.4\%$). Variability in the perceptual reports did not differ between Control and Deafferented groups [Means \pm SE, Control: $14.2^\circ \pm 2.2^\circ$; Deafferent: $15.7^\circ \pm 2.8^\circ$; $t(13) = 0.4$, $P = 0.67$, $D = 0.1$]. Negative and positive perceptual reports denote perceived movement outcomes toward or away from the perturbation (clamped cursor feedback), respectively.

Reaction time was defined as the interval from target presentation to the start of movement, marked by the cursor moving more than 1 cm from the starting annulus. Movement time was defined as the interval between the start of movement and the cursor reaching 8 cm, the target distance. If the movement time exceeded 500 ms, the message, “too slow” was displayed at the center of the screen for 750 ms before the next trial began [Means \pm SE, Control group = $4.4 \pm 0.6\%$; Deafferented group = $6.3 \pm 1.4\%$; $t(13) = 1.2$, $P = 0.27$, $D = 0.4$].

Data were statistically analyzed using a linear mixed effect model (R: lmer function) with Phase (baseline, early, late, and aftereffect) and Group (Control and Deafferented) as fixed (interacting) factors and Participant as a random factor. Post hoc two-tailed t tests on the β s from the linear mixed effect model were evaluated using the emmeans and ANOVA functions in R (Bonferroni corrected for multiple comparisons). Given the differences in sample size and group characteristics, we opted to use Welch’s t tests. This test is designed for comparing two independent groups when it cannot be assumed that the two groups have equal variances. Standard effect sizes are reported (η^2 for fixed factors; Cohen’s D_z for within-subjects t tests, Cohen’s D for between-subjects t tests).

We also used a continuous performance measure to compare the groups, implementing a cluster-based permutation test on the movement angle data [similar methods used in previous papers: (28, 36, 37)]. The test consisted of two steps. First, a t test was performed for each movement cycle across

experimental conditions to identify clusters showing a significant difference. Clusters were defined as epochs in which the P values from the t tests were less than 0.05 for at least two consecutive cycles. The F or t values were then summed up across cycles within each cluster, yielding a combined cluster score. Second, to assess the probability of obtaining a cluster of consecutive cycles with significant P values, we performed a permutation test. Specifically, we generated 1,000 permutations by shuffling the condition labels. For each shuffled permutation, we calculated the sum of the t scores. Doing this for 1,000 permutations generated a distribution of scores. The proportion of random permutations that resulted in a t score that was greater than or equal to that obtained from the data could be directly interpreted as the P value. Clusters with $P_{\text{perm}} < 0.05$ are reported.

RESULTS

Implicit Adaptation Is Minimally Impacted by Chronic Deafferentation

We compared the performance of six participants with a severe proprioceptive loss to that of 60 age-, gender-, device usage (trackpad or mouse), and laterality-matched controls on a clamped visuomotor rotation task, a method that isolates implicit adaptation (29) (Fig. 1A). Consistent with previous studies using the clamped feedback task, the control group showed a gradual change in movement angle in the opposite direction to the 30° clamped visual feedback, with the deviation averaging ~20° away from the target at the end of the clamped feedback block (Fig. 1C). The deafferented group showed a similar pattern of learning, providing a compelling demonstration that implicit adaptation is minimally impacted by the loss of proprioceptive and tactile afferents.

We analyzed the data at four phases in the experiment: baseline (with no visual cursor feedback), early adaptation (with clamped cursor feedback), late adaptation (with clamped cursor feedback), and aftereffect (with no visual cursor feedback). There was a main effect of phase [$F(3,192) = 287.0$, $P < 0.001$, $\eta^2 = 0.61$]. Implicit adaptation in response to the clamped visual feedback was observed during the early, late, and aftereffect phases [all phases vs. baseline movement angle, $t(192) > 11.0$, $P < 0.001$, $D_z > 2.8$] (Fig. 1D). Movement angle increased from early to late adaptation [$t(192) = 15.3$, $P < 0.001$, $D_z = 2.0$]. When visual feedback was eliminated during the aftereffect block, movement angle remained elevated, exhibiting only a small decrease compared with that observed late in adaptation [$t(192) = -3.4$, $P < 0.001$, $D_z = 0.6$]. This result highlights that the change in movement angle elicited by clamped feedback was implicit.

Turning to our main question, we did not observe any significant differences in the extent of implicit adaptation between the deafferented and control participants. There was neither a significant main effect of group [$F(1,159) = 0.99$, $P = 0.32$, $\eta^2 = 0.00$, $\text{BF}_{01} = 4.0$, moderate evidence for the null], nor a significant interaction between group and phase [$F(3,192) = 0.5$, $P = 0.68$, $\eta^2 = 0.00$, Bayes Factor, $\text{BF}_{01} = 6.2$, moderate evidence for the null]. In addition, the cluster-based permutation t test did not identify any significant clusters across all phases of the experiment as there were no consecutive cycles in which a t test yielded a P value less

than 0.05. Furthermore, implicit adaptation in the deafferented group was not significantly modulated by the participants' age [$r(4) = -0.2$, $P = 0.66$], sex [$t(4) = 1.1$, $P = 0.39$], handedness [$t(4) = 0.9$, $P = 0.44$], etiology [$t(4) = 1.3$, $P = 0.32$], or years since deafferentation [$r(4) = 0.7$, $P = 0.12$].

Notably, all deafferented participants exhibited a substantial aftereffect, underscoring that implicit adaptation is minimally impacted in this population.

Perceived Movement Outcome Is Minimally Impacted by Chronic Deafferentation

We next turned to the question of how perceived movement outcome was impacted by proprioceptive and tactile loss. Every 10th movement cycle, a number wheel appeared on the screen immediately after the center-out reaching movement was completed (Fig. 1B). Similar to previous studies (28), participants had to report their perceived movement outcome when the cursor crossed the target distance; to do this, they used the computer keyboard to type in the number closest to their perceived movement position. Following the report, the white cursor reappeared at a random position near the start position, cueing the participant to move the cursor back to the start position to initiate the next trial.

Perceptual reports were unbiased in baseline (denoted by near zero reports in Fig. 1E) and exhibited a shift toward the perturbed visual feedback during the clamped feedback block (denoted by negative reports). This perceived movement error, present even after only one clamped feedback cycle, can be considered to result in a learning signal driving adaptation on the next trial given the assumption that the desired movement position is at the target (per task instructions). For the control participants, the perceived error remained relatively constant across most of the adaptation block, only realigning back to the target at the end of the late adaptation phase. The deafferented group also showed a shift toward the perturbed visual feedback with the onset of the perturbed feedback, and this shift persisted throughout the adaptation block.

We analyzed the data at four phases in the experiment: baseline, early adaptation, late adaptation, and aftereffect phases. There was a main effect of phase [$F(3,192) = 7.3$, $P < 0.001$, $\eta^2 = 0.03$]. Compared with the baseline phase, perceived movement outcomes in both groups were significantly (but subtly) biased toward the visual cursor during early and late adaptation phases [early vs. baseline reports: $t(192) = -2.4$, $P = 0.02$, $D_z = 0.3$; late vs. baseline reports: $t(192) = -2.5$, $P = 0.01$, $D_z = 0.3$]. The Control group exhibited a $-3.3 \pm 1.1^\circ$ perceived error ($P = 0.02$) (i.e., change in perceived movement outcome between early and baseline phases), a value consistent with prior work (28). Notably, the Deafferented group shifted $-7.5^\circ \pm 4.5^\circ$ in the same direction ($P = 0.04$), with all but one (IW) deafferented participant exhibiting this perceived error (Fig. 1F). The magnitude of the shift was similar in the two adaptation phases [early vs. late: $t(192) = -1.7$, $P = 0.87$, $D_z = 0.03$], but dissipated when visual feedback was removed in the aftereffect phase [late vs. aftereffect: $t(192) = 4.1$, $P < 0.001$, $D_z = 0.6$; aftereffect vs. baseline: $t(192) = 1.5$, $P = 0.13$, $D_z = 0.23$].

Turning to the comparison between groups, we did not observe any significant differences in perceptual movement outcomes between the deafferented and control participants.

There was neither a significant main effect of Group [$F(1,216) = 0.9, P = 0.34, \eta^2 = 0.04, BF_{01} = 0.5$; anecdotal evidence in favor of the null) nor a significant interaction between Group and Phase [$F(3,192) = 0.95, P = 0.95, \eta^2 = 0.0, BF_{01} = 6.8$; strong evidence in favor of the null]. Furthermore, perceptual reports in the deafferented group were not significantly modulated by the participants' age [$r(4) = 2.7, P = 0.06$], sex [$t(4) = 2.3, P = 0.13$], handedness [$t(4) = -2.3, P = 0.13$, etiology [$t(4) = 0.5, P = 0.67$], or years since deafferentation [$r(4) = 2.4, P = 0.07$]. Thus, deafferented individuals exhibited similar biases in perceived movement outcome as the control individuals. Although our findings indicate that proprioceptive loss has minimal impact on perceived movement outcome, there are several limitations to these perceptual reports, an issue we address in DISCUSSION.

Motor Control Impairments in Deafferented Individuals

To evaluate motor performance in deafferented individuals in this task, we focused on the kinematic data from the baseline phase without visual feedback. As shown in Fig. 2, there were no significant group differences in movement time [Control: 102.0 ± 10.1 ms, Deafferented: 92.3 ± 12.3 ms; $t(14) = 0.6, P = 0.6, D = 0.1$]. Moreover, neither group showed a significant bias in movement angle during the baseline block [baseline vs. 0: Controls, $t(59) = -0.4, P = 0.69, D_z = 0.1$; Deafferented: $t(5) = -0.8, P = 0.46, D_z = 0.1$].

However, baseline movement angle variability was larger in the Deafferented group compared with the Control group [signed movement angle SD: Control: $6.4^\circ \pm 0.4^\circ$, Deafferented: $8.9^\circ \pm 0.9^\circ$; $t(7) = 2.7, P = 0.03, D = 0.9$; unsigned movement angle SD: Control: $4.1^\circ \pm 0.3^\circ$, Deafferented: $5.3^\circ \pm 0.4^\circ$; $t(11) = 2.5, P = 0.03, D = 0.6$], indicating that movements were less consistent when proprioception was impaired. This impairment in the deafferented group was also not significantly modulated by the participants' age [$r(4) = -0.006, P = 0.91$], sex [$t(4) = 0.8, P = 0.58$], handedness [$t(4) = 0.9, P = 0.44$], etiology [$t(4) = 0.8, P = 0.48$], or years since deafferentation [$r(4) = 1.0, P = 0.36$].

Given this difference, we repeated our between-group analysis of implicit adaptation and included movement angle variability as a covariate. There was neither a significant main effect of Group [$F(1,154) = 0.1, P = 0.74, \eta^2 = 0.00$], nor a significant interaction between Variability and

Group [$F(3,193) = 0.7, P = 0.57, \eta^2 = 0.01$]. Thus, even though deafferented adults exhibited greater movement variability, deafferentation had minimal impact on implicit adaptation and perceived movement outcome.

DISCUSSION

Summary of Results

Individuals lacking proprioceptive and tactile inputs provide an important test case for understanding the role of proprioception in implicit adaptation. Although previous case studies have observed preserved motor adaptation in deafferented adults (20, 21, 24–27), these studies did not use tasks that isolated implicit adaptation. To address this, we used a modified visuomotor rotation task to cleanly examine implicit motor adaptation and probe perceived movement outcome in deafferented adults. We found that the deafferented group exhibited robust implicit adaptation and perceived movement outcome toward the visual perturbation. Moreover, we did not observe any behavioral differences on these measures between the deafferented and control groups. These findings underscore how proprioceptive loss has minimal impact on the extent of implicit motor adaptation and perceived movement outcome.

Theoretical Considerations

Our study is the first, to the best of our knowledge, to examine perceived movement outcomes during motor adaptation in deafferented participants. In control subjects, perceived outcomes are a multimodal percept that relies on visual and proprioceptive feedback, as well as predictive information arising from prior expectations associated with the intended aim and a sensory prediction derived from the efferent motor command (7–10, 14). We hypothesized that the loss of proprioception in deafferented adults would lead to a greater reliance on vision for determining perceived outcomes. However, our results showed that perceptual outcomes did not significantly differ between the control and deafferented groups.

The lack of significant differences between deafferented and control participants appears to align with a visuo-centric model of implicit adaptation. According to this view, implicit adaptation is driven by a visual error—the difference between the predicted and actual visual feedback (29, 38). Since this model

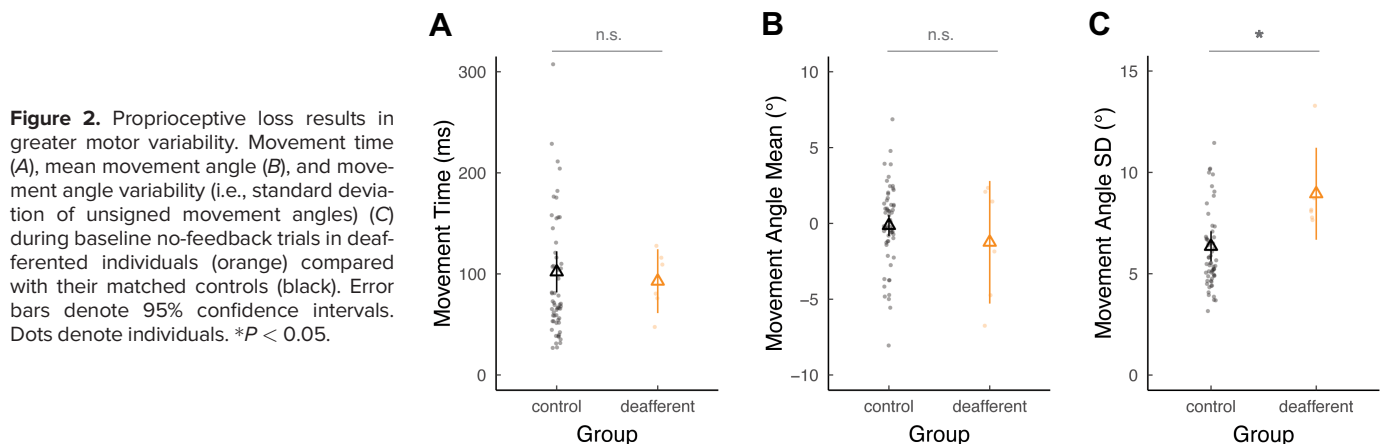


Figure 2. Proprioceptive loss results in greater motor variability. Movement time (A), mean movement angle (B), and movement angle variability (i.e., standard deviation of unsigned movement angles) (C) during baseline no-feedback trials in deafferented individuals (orange) compared with their matched controls (black). Error bars denote 95% confidence intervals. Dots denote individuals. $*P < 0.05$.

does not include proprioception, deafferentation would not be expected to impact implicit adaptation. However, the model has its shortcomings. For example, it fails to explain why the proprioceptive variability and proprioceptive biases correlate with the extent of implicit adaptation (39–41).

Alternatively, implicit adaptation in deafferented adults might reflect the operation of compensatory mechanisms associated with chronic proprioceptive loss. According to the perceptual realignment model, visual and proprioceptive feedback, along with predictive signals from efference copy and prior knowledge contribute to form a unified perception of movement location. When a visual perturbation is introduced, the perceived movement location shifts toward the visual input. In control participants, this shift might result from recalibrating proprioceptive signals and/or efferent-based predictions. The situation could be different in deafferented individuals, especially when they have lived with the condition for a long time. In such cases, visual and predictive information may be weighted more heavily (12, 14, 20, 42–44). Our data suggest that integrating sensory predictions—the prior expectations associated with the intended aim and/or the sensory prediction derived from the efferent motor command—with biased/perturbed visual feedback may be sufficient to create a perceived movement error that drives implicit adaptation (14).

Future studies using methods to transiently disrupt proprioception in healthy controls would provide one way to evaluate the merits of a visuo-centric view and our perceptual realignment model. Specifically, the visuo-centric hypothesis would predict that transient disruption of proprioception—induced peripherally by muscle vibration (45, 46) or centrally through noninvasive brain stimulation (47–50) would have no impact on implicit adaptation. In contrast, assuming that reweighting is a gradual process, the perceptual realignment model predicts that transient disruption of proprioception would heighten implicit adaptation. Furthermore, using functional magnetic resonance imaging (fMRI), the perceptual realignment model predicts that deafferented participants, compared with controls, would exhibit less activation in brain areas conveying proprioceptive information (e.g., the primary somatosensory cortex) and more activation in brain areas conveying efferent-based sensory predictions (e.g., the cerebellum) and visual information (e.g., primary visual cortex) throughout the implicit adaptation.

Study Limitations

Although we have recruited one of the largest cohorts of rare deafferented participants to examine the effect of proprioceptive loss on implicit adaptation (previous studies consist of case studies), the results remain limited by the small sample size. Future studies could explore whether implicit adaptation is impacted in patients with more prevalent forms of neuropathy, such as those induced by chemotherapy or diabetes, although such conditions tend to produce less severe forms of proprioceptive loss. A larger sample would provide a more robust means to evaluate not only whether proprioceptive impairment modulates adaptation but also provide a means to ask about modulating variables such as the duration of deafferentation.

We failed to find heightened perceived movement errors in deafferented adults. There are at least two potential

explanations for this null result. First, although the deafferentation was severe, the proximal muscles of the upper extremity were possibly spared in a subset of our participants. As such, residual proprioceptive input might have limited the magnitude of the perceived error. Future studies should use careful experimental designs and detailed kinematic analyses to ensure that the task relies solely on the wrist and elbow movements as well as provide a more thorough characterization of participants' deafferentation.

Second, participants might have used peripheral vision of their actual hand position, and such visual input could impact both adaptation and perceptual reports. We conducted this study during the global pandemic that prevented us from being physically present. We considered asking the participants to perform the task without direct vision of the hand but based on our combined experience working with deafferented patients (20, 21, 26), we anticipated that participants would struggle to return to the start position without seeing their hand, potentially making the task frustrating. Empirically, this concern could be addressed in future experiments in a controlled laboratory setting where we could occlude vision of the hand and passively assist participants in returning to the start position with a robotic manipulandum (21, 24, 41).

Although peripheral vision may be crucial for some aspects of motor control (51–54), prior literature suggests that it does not play a major role in sensorimotor adaptation (55, 56). First, participants tend to focus on the visual target throughout the movement rather than on their hand position during motor adaptation (56–62). Second, movement kinematics, such as movement time and variability, appear unaffected by the visibility of the hand (63, 64), implying that peripheral visual information about one's hand position may not be critical for generating a feedforward motor plan. Third, our online results with peripheral vision available align closely with in-laboratory results where peripheral vision was not possible (35, 65). Nonetheless, we cannot rule out the possibility that individuals used peripheral vision in the present study. Future studies incorporating eye-tracking technology would be instrumental in determining the extent to which peripheral vision is used by both deafferented and control groups.

Moreover, although there are notable kinematic differences between using a mouse and a trackpad (66, 67), we do not believe that our results were substantially affected by the use of different computer devices. Specifically, in a data set comprising 2,000 individuals who were tested with our home-based online platform, we did not observe significant differences in implicit adaptation between those who used trackpad and those who used a mouse (35, 65). The results of this study and others using the online platform suggest that the present results are unlikely to be affected because of our remote testing method. We (68, 69) and other laboratories (70–73) have successfully replicated many classic adaptation phenomena by conducting studies remotely. Therefore, this method offers the unique advantage of conducting sensorimotor experiments with deafferented participants, or more generally, participants with movement disorders, who may find it difficult and inconvenient to travel to a laboratory setting, especially when there are constraints on in-person data collection (i.e., the COVID global pandemic).

In previous studies involving reports of perceived movement outcome during adaptation, the perceived error reached a maximum value shortly after the onset of the visual perturbation and then dissipated over time, returning to baseline levels in the last phase of adaptation (28, 74). Although this pattern was evident in the mean data for the control participants, there was no statistical reduction in the perceived movement error between the early and late adaptation phases. Several factors might account for this observation: First, the study's duration may have been too short. Specifically, our experiment spanned 1.5 h and consisted of 440 trials. This design choice was made to minimize fatigue and cater to the mobility challenges faced by the deafferented participants. Extending the number of learning trials and perceptual probes may clarify whether the perceived error diminishes as implicit adaptation ceases.

Second, the perceptual probes in our study may have been subject to unaccounted influences such as gaze direction (75), transformations across horizontal and vertical workspaces, participants' interpretations of the directive to "ignore the visual cursor," and the presence of a visual target. That is, participants, both controls and patients, might have been inclined to base their perceptual reports on the location of the visual target and clamped visual feedback, rather than on efferent and/or proprioceptive feedback conveying hand position. To obtain a more precise measure, future studies could examine perceived movement outcome after a passive or self-initiated movement, in the absence of both a visual cursor and target (76).

Conclusions

Our findings indicate that chronic proprioceptive loss has minimal impact on implicit motor adaptation and perceived movement outcome, posing a challenge for theoretical models of adaptation that involve proprioception.

DATA AVAILABILITY

All raw data and code are available on Dryad: <https://datadryad.org/stash/dataset/doi:10.6078/D19T4V>.

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DISCLOSURES

R.B.I. is a co-founder with equity in Magnetic Tides, Inc., a biotechnology company created to develop a novel method of non-invasive brain stimulation. None of the other authors has any conflicts of interest, financial or otherwise, to disclose.

AUTHOR CONTRIBUTIONS

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

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