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HAL Authorization

1 Minimal impact of chronic proprioceptive loss on implicit sensorimotor adaptation
2 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 re-alignment 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 outcome throughout the experiment. Surprisingly, both implicit adaptation and perceived movement outcome were minimally impacted by chronic deafferentation, posing a challenge to the perceptual re-alignment 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.

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 re-alignment model¹, the perceived movement outcome is a multimodal percept. Feedback can be provided from visual and proprioceptive receptors (i.e., muscle 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 (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

¹In the original exposition of this model, we used the term “proprioceptive re-alignment”. 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 re-alignment” to better capture this idea.

73 implicit motor adaptation. Deafferentation, which can result from either a congenital disorder or a
74 neurological insult, is rare (16–23). Previous case studies have shown that motor adaptation is minimally
75 impacted in deafferented adults (20, 21, 24–27). However, the tasks used in these studies did not isolate
76 implicit adaptation, meaning learning performance could also be influenced by explicit, strategic
77 processes (25, 28). This makes it challenging to determine whether implicit adaptation is reduced,
78 minimally impacted, or even enhanced compared to controls. Moreover, the impact of proprioceptive loss
79 on the perceived movement outcome during implicit adaptation is unknown.

80
81 To fill this gap, we tested a cohort of deafferented individuals on a clamped visuomotor rotation task that
82 isolates implicit adaptation and probes perceived movement outcome (29, 30) (Figure 1A). In this task,
83 participants reach to a visual target and the visual feedback (i.e., a white cursor on the computer screen)
84 follows a fixed trajectory defined relative to the target. Thus, unlike standard perturbation methods, the
85 direction of the visual feedback is not contingent on the participant’s movement direction. Participants are
86 fully informed of this manipulation and instructed to always reach directly to the target while ignoring the
87 visual feedback. Despite these explicit instructions, the visual perturbation between the position of the
88 target and the cursor elicits an implicit adaptive response in healthy participants, causing a gradual trial-
89 by-trial change in movement direction away from the target and in the opposite direction to the visual
90 cursor. These motor adjustments are not the result of explicit re-aiming; indeed, participants are oblivious
91 to the change in their movement (29). Furthermore, participants were periodically asked to report their
92 perceived movement outcome using a wheel of numbers (Figure 1B), providing a measure of their
93 perceived movement error – the distance between the perceived movement outcome and the visual target.

94
95 Based on the perceptual re-alignment model, we tested two core predictions. First, there should be a
96 heightened perceived error in the deafferented group compared to that of the control group. With the loss
97 of proprioception, we predicted the deafferented group would rely heavily on visual feedback of the
98 cursor to determine perceived movement outcome and thus show a heightened perceived movement error.
99 Consequently, an increase in the perceived movement error in the deafferented group would result in
100 heightened implicit adaptation, requiring a larger change in movement angle to offset the larger error.

101 Methods

103 *Ethics Statement*

104
105 All participants gave written informed consent in accordance with policies approved by the UC
106 Berkeley's Institutional Review Board. Participation in the study was in exchange for monetary
107 compensation.

109 *Participants*

110
111 We recruited deafferented participants who, despite their severe upper-limb sensory loss, could perform a
112 simple reaching task. Given the rarity of this condition as well as issues with functional mobility, we used
113 an online approach to test six chronic, deafferented participants spread across four countries (Tables 1-2).
114 This sample is larger and more etiologically diverse than those recruited in prior studies. All deafferented
115 participants reported having corrected or uncorrected vision greater than 19/20.

116
117 While there are no definitive standards for clinically evaluating proprioception, we reviewed the medical
118 reports for each deafferented participant. For all the patients, the reports indicated loss of somatosensory
119 reflexes and proprioceptive loss in the hand and in the forearm. Abnormalities were noted on
120 proprioceptive position matching tasks (wrist, elbow, shoulder), tactile discrimination tasks, and vibration
121 perception. The reports noted severe ataxia while performing pegboard tests and when writing with their
122 dominant hand. All deafferented participants had severe gait impairments and, except for CD, all required
123 support for their daily needs (walker, wheelchair, or a caretaker).

124
125 Below, we detail the specific clinical etiologies for each participant. Note that all the participants with
126 acquired deafferentation have previously participated in other studies. For further details on their clinical
127 presentations, we refer readers to the cited references. The three participants with congenital
128 deafferentation have impaired proprioceptive and tactile perception, resulting in severe motor ataxia: CM
129 and SB have an autosomal recessive mutation in the mechanoreceptor PIEZO2 gene (19), while CD has
130 an inherited mutation in the mechanoreceptor ASIC3 gene (31).

131
132 The three other participants acquired deafferentation following an acute neurological episode. IW
133 suffered a sensory neuropathy at age 19 from an autoimmune response to a viral infection, resulting in
134 severe proprioceptive and tactile impairment below the neck (18, 32). WL experienced a bout of
135 polyradiculitis at age 31, leading to severe proprioceptive and tactile impairments below the neck (21,
136 33). DC has severe proprioceptive impairment in the right upper limb subsequent to surgical resection of
137 a vascular tumor at age 38 near the right medulla oblongata (22, 34).

138
139 A total of 60 control participants were recruited to closely match each of the deafferented participants in
140 terms of age, sex, handedness, and device used in the experiment (Table 2). Previous studies on
141 deafferented participants typically recruit five controls per patient (21, 35). To ensure a more conservative
142 and robust sample, we opted to double this number to 10 in our study. Control participants were recruited
143 via Prolific, an online crowdsourcing platform that connects researchers with willing participants
144 worldwide. This platform allows us to find control participants closely matched to deafferented
145 participants in terms of age, sex, handedness, and preferred device used (mouse or trackpad) in daily life.
146 All control participants reported to have corrected or uncorrected 20/20 vision.

147
148 The deafferented participants completed the task during a live video session, with the experimenter
149 available to provide instructions and monitor performance. The control participants completed the task
150 autonomously, accessing the website at their convenience.

151

Name	Etiology	Age	Years since onset	Sex	Handedness
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

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Table 1: Deafferented participant demographics. Participants identified as either male (M) or female (F), right-handed (R) or left-handed (L).

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

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Table 2: Deafferented and age, sex, handedness, and device-matched control participants. Participants either used 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: $\chi^2(1, 66) = 0.3, p = 0.59$).

Apparatus

Participants used their own computer to access a dynamic webpage (HTML, JavaScript, and CSS) hosted on Google Firebase (36). 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 x height: 1455 x 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 (36).

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 ($45^\circ, 135^\circ, 225^\circ, 315^\circ$ 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 cm – 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).

193
194 At the beginning of each trial, the cursor appeared at a random position within 1 cm of the center of the
195 screen. As such, the actual starting position varied subtly from trial to trial. The participant initiated the
196 trial by moving the cursor to the center start location. After maintaining the cursor in the start position for
197 500 ms, the target appeared. Participants were instructed to move rapidly, attempting to “slice” through
198 the target. There were three types of feedback cursor conditions during the experiment: No visual
199 feedback, veridical visual feedback, and clamped visual feedback. During no-feedback trials, the cursor
200 was extinguished as soon as the movement left the start annulus and remained off for the entire
201 movement. During veridical feedback trials, the movement direction of the cursor was veridical with
202 respect to the participants’ movement direction. The veridical cursor was extinguished when the computer
203 pointer (i.e., the veridical representation of the fingertip position in trackpad or mouse coordinates on the
204 computer screen) crossed the radial target distance of 8 centimeters. Veridical feedback trials were only
205 used at the beginning of the experiment to familiarize the participant with the task. During clamped
206 feedback trials (Figure 1A), the cursor moved at a 30° angular offset relative to the position of the target,
207 counterclockwise and irrespective of the participant’s actual movement direction – a manipulation used to
208 isolate implicit adaptation (29, 30). The clamped cursor was extinguished when the movement distance
209 exceeded the radial target distance of 8 centimeters.
210

211 Every 10th cycle, participants were asked to report their perceived movement outcome for four
212 consecutive trials (i.e., one report per target location). There was a total of 40 ‘perceptual report’ trials
213 over the course of the experiment. On perceptual report trials, a number wheel appeared on the screen as
214 soon as the clamped cursor reached the target amplitude, cueing the participant for a report. The numbers
215 (“1” to “60”) increased incrementally in the clockwise direction (spaced at 6° intervals around the circle),
216 with the number “1” positioned at the target location. With their non-dominant hand, the participant used
217 the keyboard to report the number closest to their perceived movement position. Following the report, the
218 white cursor appeared at a random position within 1 cm of the center start position. The participant moved
219 the cursor to the start position to initiate the next trial.
220

221 The main task consisted of 110 cycles (four movements per cycle, 440 trials total) distributed across three
222 main blocks of cycles/trials: A no-feedback block (40 cycles; 160 trials to assess baseline performance),
223 clamped feedback block (60 cycles; 240 trials to assess adaptation), and a no-feedback block (10 cycles;
224 40 trials to assess aftereffects). Prior to the clamped feedback block, the following instructions were
225 provided: “The white cursor will no longer be under your control. Please ignore the white cursor and
226 continue to aim directly towards the target.”
227

228 To clarify the invariant nature of the clamped feedback, eight demonstration trials were provided before
229 the first clamped perturbation block. On all eight trials, the target either appeared straight ahead (90°
230 position), and the participant was told to move to the left, to the right, and backward. On all these
231 demonstration trials, the cursor moved in a straight line, 90° offset from the target. In this way, the
232 participant could see that the spatial trajectory of the cursor was unrelated to their own movement
233 direction.
234

235 To verify that the participants understood the clamped visual feedback manipulation task, we included an
236 instruction check after eight demonstration trials in the adaptation block. The following sentence was
237 presented on the screen: “Identify the correct statement. Press ‘a’: I will aim away from the target and
238 ignore the white dot. Press ‘b’: I will aim directly towards the target location and ignore the white dot.”
239 The experiment only progressed if participants pressed the “b” key. Indeed, all participants understood the
240 instructions and pressed “b” to proceed.
241

242 *Data analysis*

243

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

254
255 We defined four phases of adaptation: Baseline, early adaptation, late adaptation, and aftereffect. Baseline
256 performance was operationalized as the mean movement angle over the no-feedback baseline block
257 (cycles 1 – 40), providing a measure of stable baseline performance. Early adaptation was operationalized
258 as the mean movement angle over the first 20 cycles of the clamped visual feedback block (cycles 41 –
259 60), capturing the steepest portion of the learning curve. Late adaptation was defined as the mean
260 movement angle over the last 20 cycles of the clamped visual feedback block (cycles 81 – 100),
261 representing the stable asymptotic phase of the learning curve. The aftereffect was operationalized as the
262 mean movement angle over all 10 cycles of the no-feedback aftereffect block (cycles 101 – 110).

263
264 Outlier responses were defined as trials in which the movement angle was greater than 90° from the target
265 or deviated more than three standard deviations from a trendline constructed with a moving 5-trial
266 window. Outlier trials were excluded from further analysis since behavior on these trials could reflect
267 anticipatory movements to the wrong target or attentional lapses (average excluded movement trials:
268 Control group = $1.3 \pm 0.2\%$; Deafferented group = $1.1 \pm 0.3\%$).

269
270 The perceptual reports provide the dependent variable for measuring the perceived movement outcome.
271 These data were converted into angular values, although we note that the perceptual reports involve
272 categorical data (numbers spaced at 6° intervals), whereas in angular form they suggest a continuous
273 variable. Outlier responses were removed in the exact same manner as the movement angle data (average
274 excluded report trials: Control group = $1.8 \pm 1.0\%$; Deafferented group = $0.4 \pm 0.4\%$). Variability in the
275 perceptual reports did not differ between Control and Deafferented groups (Mean \pm SEM, Control: 14.2°
276 $\pm 2.2^\circ$; Deafferent: $15.7^\circ \pm 2.8^\circ$; $t(13) = 0.4, p = 0.67, D = 0.1$). Negative and positive perceptual
277 reports denote perceived movement outcomes toward or away from the perturbation (clamped cursor
278 feedback), respectively.

279
280 Reaction time was defined as the interval from target presentation to the start of movement, marked by
281 the cursor moving more than 1 cm from the starting annulus. Movement time was defined as the interval
282 between the start of movement and the cursor reaching 8 cm, the target distance. If the movement time
283 exceeded 500 ms, the message, “too slow” was displayed at the center of the screen for 750 ms before the
284 next trial began (Mean \pm SEM, Control group = $4.4 \pm 0.6\%$; Deafferented group = $6.3 \pm 1.4\%$; $t(13) =$
285 $1.2, p = 0.27, D = 0.4$).

286
287 Data were statistically analyzed using a linear mixed effect model (R: lmer function) with Phase
288 (baseline, early, late, and aftereffect) and Group (Control and Deafferented) as fixed (interacting) factors
289 and Participant as a random factor. Post hoc two-tailed t-tests on the betas from the linear mixed effect
290 model were evaluated using the emmeans and ANOVA functions in R (Bonferroni corrected for multiple
291 comparisons). Given the differences in sample size and group characteristics, we opted to use Welch’s t-
292 tests. This test is designed for comparing two independent groups when it cannot be assumed that the two

293 groups have equal variances. Standard effect sizes are reported (η^2 for fixed factors; Cohen's D_z for
294 within-subjects t-tests, Cohen's D for between-subjects t-tests).

295
296 We also used a continuous performance measure to compare the groups, implementing a cluster-based
297 permutation test on the movement angle data (similar methods used in previous papers: (29, 37, 38)). The
298 test consisted of two steps. First, a t-test was performed for each movement cycle across experimental
299 conditions to identify clusters showing a significant difference. Clusters were defined as epochs in which
300 the p-value from the t-tests were less than 0.05 for at least two consecutive cycles. The F or t values were
301 then summed up across cycles within each cluster, yielding a combined cluster score. Second, to assess
302 the probability of obtaining a cluster of consecutive cycles with significant p-values, we performed a
303 permutation test. Specifically, we generated 1000 permutations by shuffling the condition labels. For each
304 shuffled permutation, we calculated the sum of the t-scores. Doing this for 1000 permutations generated a
305 distribution of scores. The proportion of random permutations which resulted in a t-score that was greater
306 than or equal to that obtained from the data could be directly interpreted as the p-value. Clusters with p_{perm}
307 < 0.05 are reported.

308
309 *Data availability*

310 All raw data and code are available on Dryad: <https://datadryad.org/stash/dataset/doi:10.6078/D19T4V>
311

Results

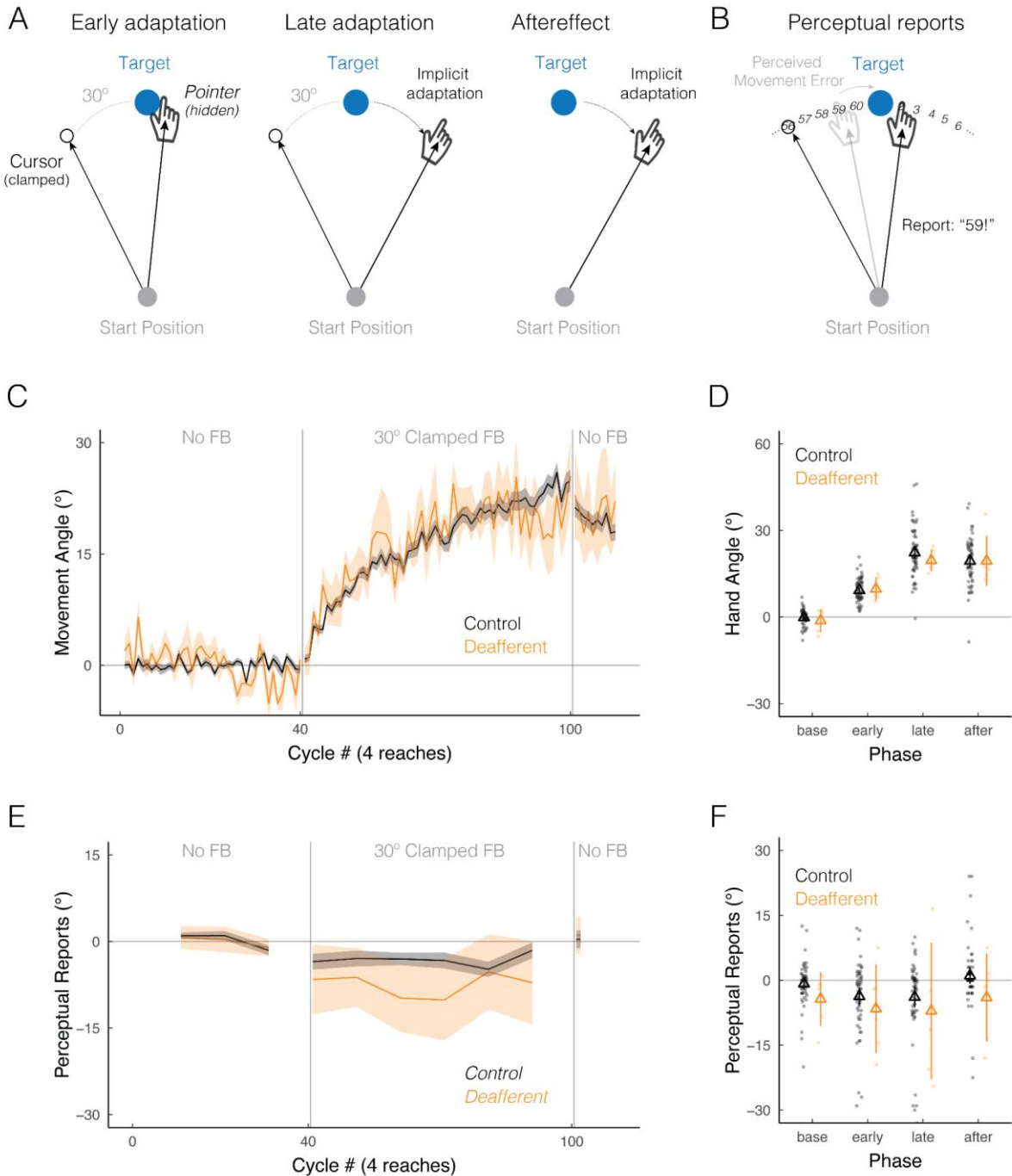
Implicit adaptation is minimally impacted by chronic deafferentation

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 (30) (Figure 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 (Figure 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, $t(192) > 11.0, p < 0.001, D_z > 2.8$) (Figure 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 to 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 ($F(1, 159) = 0.99, p = 0.32, \eta^2 = 0.00, BF_{01} = 4.0$, moderate evidence for the null), nor a significant interaction between group and phase ($F(3, 192) = 0.5, p = 0.68, \eta^2 = 0.00, BF_{01} = 6.2$, moderate evidence for the null). Additionally, 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.



349
350

351 **Figure 1: Minimal impact of proprioceptive loss on implicit motor adaptation and perceived movement**
 352 **outcome.** (A) Schematic of the visual clamped feedback task. After baseline trials without visual cursor feedback
 353 (cycles 1 – 40), participants were exposed to 240 trials with clamped visual feedback (cycles 41 – 100) in which the
 354 cursor (white circle) followed a fixed trajectory, rotated 30° counterclockwise relative to the target and irrespective
 355 of the participant’s movement. Participants were instructed to always move their pointer (hidden or visible) directly
 356 to the target (blue circle) and ignore the visual clamped cursor feedback. The pointer represents the veridical
 357 representation of the fingertip position in trackpad or mouse coordinates on the computer screen. Left, middle and
 358 right panels are schematics of pointer and cursor positions during the early (cycles 41–60), late (cycles 81–100), and
 359 aftereffect (cycles 101–110) phases of adaptation, respectively. (B) Every 10th cycle, participants reported their

360 perceived movement outcome. On these trials, a number wheel would appear on the screen as soon as the amplitude
361 of the movement reached the target distance, cueing participants for a report (top panel). The numbers (“1” to “60”)
362 increased incrementally in the clockwise direction (spaced at 6° intervals around the circle), with the number “1”
363 positioned at the target location. Participants used their keyboard to type the number closest to their perceived
364 movement outcome when reaching the target distance. Mean time courses of movement angle (C) and perceptual
365 reports (E) for Control (black; N = 60) and Deafferented groups (orange; N = 6). Shaded areas represent standard
366 error. Both measures are presented relative to the target (0°); negative and positive values denote movements/reports
367 toward or away from the cursor, respectively. One cycle consisted of four movements, one to each of the four
368 possible target locations. Summary of implicit adaptation (D) and perceptual report data (F) over baseline, early, late
369 and aftereffect phases. Error bars denote 95% confidence intervals. Triangle denotes the mean for each group. Dots
370 denote individuals.

371

372 *Perceived movement outcome is minimally impacted by chronic deafferentation*

373

374 We next turned to the question of how perceived movement outcome was impacted by proprioceptive and
375 tactile loss. Every 10th movement cycle, a number wheel appeared on the screen immediately after the
376 center-out reaching movement was completed (Figure 1B). Similar to previous studies (29), participants
377 had to report their perceived movement outcome when the cursor crossed the target distance; to do this,
378 they used the computer keyboard to type in the number closest to their perceived movement position.
379 Following the report, the white cursor reappeared at a random position near the start position, cueing the
380 participant to move the cursor back to the start position to initiate the next trial.

381

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

391

392 We analyzed the data at four phases in the experiment: baseline, early adaptation, late adaptation, and
393 aftereffect phases. There was a main effect of phase ($F(3, 192) = 7.3, p < 0.001, \eta^2 = 0.03$). Compared
394 to the baseline phase, perceived movement outcomes in both groups were significantly (but subtly) biased
395 toward the visual cursor during early and late adaptation phases (early vs baseline reports: $t(192) =$
396 $-2.4, p = 0.02, D_z = 0.3$; late vs baseline reports: $t(192) = -2.5, p = 0.01, D_z = 0.3$). The Control
397 group exhibited a $-3.3 \pm 1.1^\circ$ perceived error ($p = 0.02$) (i.e., change in perceived movement outcome
398 between early and baseline phases), a value consistent with prior work (29). Notably, the Deafferented
399 group shifted $-7.5^\circ \pm 4.5^\circ$ in the same direction ($p = 0.04$), with all but one (IW) deafferented participant
400 exhibiting this perceived error (Figure 1F). The magnitude of the shift was similar in the two adaptation
401 phases (early vs late: $t(192) = -1.7, p = 0.87, D_z = 0.03$), but dissipated when visual feedback was
402 removed in the aftereffect phase (late vs aftereffect: $t(192) = 4.1, p < 0.001, D_z = 0.6$; aftereffect vs
403 baseline: $t(192) = 1.5, p = 0.13, D_z = 0.2$).

404

405 Turning to the comparison between groups, we did not observe any significant differences in perceptual
406 movement outcome between the deafferented and control participants. There was neither a significant
407 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
408 the null) nor a significant interaction between Group and Phase ($F(3, 192) = 0.95, p = 0.95, \eta^2 =$
409 $0.0, BF_{01} = 6.8$; strong evidence in favor of the null). Furthermore, perceptual reports in the deafferented
410 group were not significantly modulated by the participants’ age ($r(4) = 2.7, p = 0.06$), sex ($t(4) =$

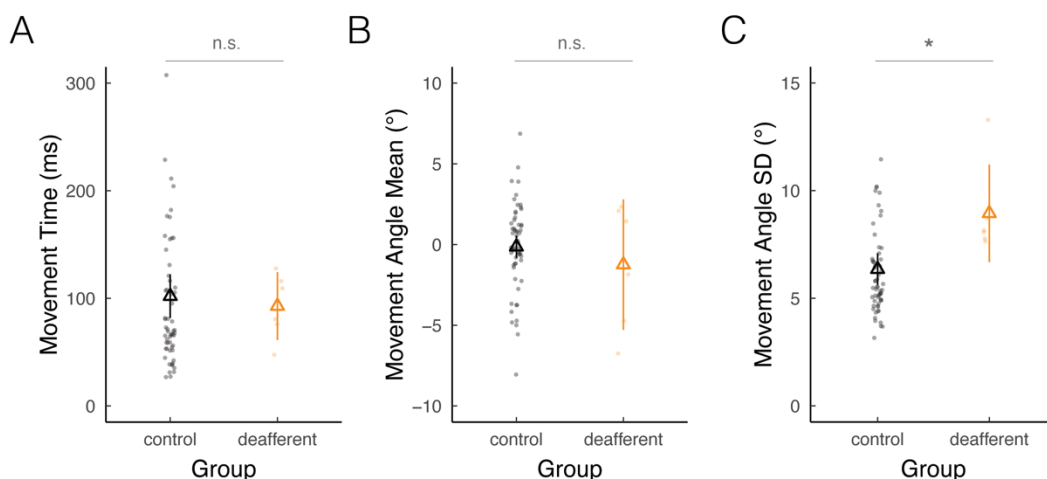
411 2.3, $p = 0.13$), handedness ($t(4) = -2.3, p = 0.13$), etiology ($t(4) = 0.5, p = 0.67$), or years since
412 deafferentation ($r(4) = 2.4, p = 0.07$). Thus, deafferented individuals exhibited similar biases in
413 perceived movement outcome as the control individuals. While our findings indicate that proprioceptive
414 loss has minimal impact on perceived movement outcome, there are several limitations to these
415 perceptual reports, an issue we address in the Discussion.

416 417 *Motor control impairments in deafferented individuals*

418
419 To evaluate motor performance in deafferented individuals in this task, we focused on the kinematic data
420 from the baseline phase without visual feedback. As shown in Figure 2, there were no significant group
421 differences in movement time (Control: 102.0 ± 10.1 ms, Deafferented: 92.3 ± 12.3 ms; $t(14) =$
422 $0.6, p = 0.60, D = 0.1$). Moreover, neither group showed a significant bias in movement angle during
423 the baseline block (baseline vs 0: Controls, $t(59) = -0.4, p = 0.69, D_z = 0.1$; Deafferented: $t(5) =$
424 $-0.8, p = 0.46, D_z = 0.1$).

425
426 However, baseline movement angle variability was larger in the Deafferented group compared to the
427 Control group (signed movement angle SD: Control: $6.4 \pm 0.4^\circ$, Deafferented: $8.9 \pm 0.9^\circ$; $t(7) =$
428 $2.7, p = 0.03, D = 0.9$; un-signed movement angle SD: Control: $4.1 \pm 0.3^\circ$, Deafferented: $5.3 \pm 0.4^\circ$;
429 $t(11) = 2.5, p = 0.03, D = 0.6$), indicating that movements were less consistent when proprioception
430 was impaired. This impairment in the deafferented group was also not significantly modulated by the
431 participants' age ($r(4) = -0.06, p = 0.91$), sex ($t(4) = 0.8, p = 0.58$), handedness ($t(4) = 0.9, p =$
432 0.44), etiology ($t(4) = 0.8, p = 0.48$), or years since deafferentation ($r(4) = 1.0, p = 0.36$).

433
434 Given this difference, we repeated our between-group analysis of implicit adaptation and included
435 movement angle variability as a covariate. There was neither a significant main effect of Group
436 ($F(1, 154) = 0.1, p = 0.74, \eta^2 = 0.00$), nor a significant interaction between Variability and Group
437 ($F(3, 193) = 0.7, p = 0.57, \eta^2 = 0.01$). Thus, even though deafferented adults exhibited greater
438 movement variability, deafferentation had minimal impact on implicit adaptation and perceived
439 movement outcome.
440



441
442 **Figure 2: Proprioceptive loss results in greater motor variability.** (A) Movement time, (B) mean movement
443 angle, and (C) movement angle variability (i.e., standard deviation of unsigned movement angles) during baseline
444 no-feedback trials in deafferented individuals (orange) compared their matched controls (black). Error bars denote
445 95% confidence intervals. Dots denote individuals. * denotes $p < 0.05$.

446 Discussion

447 *Summary of results*

449
450 Individuals lacking proprioceptive and tactile inputs provide an important test case for understanding the
451 role of proprioception in implicit adaptation. While previous case studies have observed preserved motor
452 adaptation in deafferented adults (20, 21, 24–27), these studies did not use tasks that isolated implicit
453 adaptation. To address this, we used a modified visuomotor rotation task to cleanly examine implicit
454 motor adaptation and probe perceived movement outcome in deafferented adults. We found that the
455 deafferented group exhibited robust implicit adaptation and perceived movement outcome toward the
456 visual perturbation. Moreover, we did not observe any behavioral differences on these measures between
457 the deafferented and control groups. These findings underscore how proprioceptive loss has minimal
458 impact on the extent of implicit motor adaptation and perceived movement outcome.

459 *Theoretical considerations*

461
462 Our study is the first, to the best of our knowledge, to examine perceived movement outcomes during
463 motor adaptation in deafferented participants. In control subjects, perceived outcomes are a multimodal
464 percept that relies on visual and proprioceptive feedback, as well as predictive information arising from
465 prior expectations associated with the intended aim and a sensory prediction derived from the efferent
466 motor command (7–10, 14). We hypothesized that the loss of proprioception in deafferented adults would
467 lead to a greater reliance on vision for determining perceived outcomes. However, our results showed that
468 perceptual outcome did not significantly differ between the control and deafferented groups.

469
470 The lack of significant differences between deafferented and control participants appears to align with a
471 visuo-centric model of implicit adaptation. According to this view, implicit adaptation is driven by a
472 visual error – the difference between the predicted and actual visual feedback (30, 39). Since this model
473 does not include proprioception, deafferentation would not be expected to impact implicit adaptation.
474 However, the model has its shortcomings. For example, it fails to explain why the proprioceptive
475 variability and proprioceptive biases correlate with the extent of implicit adaptation (40–42).

476
477 Alternatively, implicit adaptation in deafferented adults might reflect the operation of compensatory
478 mechanisms associated with chronic proprioceptive loss. According to the perceptual re-alignment model,
479 visual and proprioceptive feedback, along with predictive signals from efference copy and prior
480 knowledge contribute to form a unified perception of movement location. When a visual perturbation is
481 introduced, the perceived movement location shifts toward the visual input. In control participants, this
482 shift might result from recalibrating proprioceptive signals and/or efferent-based predictions. The
483 situation could be different in deafferented individuals, especially when they have lived with the
484 condition for a long time. In such cases, visual and predictive information may be weighted more heavily
485 (12, 14, 20, 43–45). Our data suggest that integrating sensory predictions – the prior expectations
486 associated with the intended aim and/or the sensory prediction derived from the efferent motor command
487 – with biased/perturbed visual feedback may be sufficient to create a perceived movement error that
488 drives implicit adaptation (14).

489
490 Future studies using methods to transiently disrupt proprioception in healthy controls would provide one
491 way to evaluate the merits of a visuo-centric view and our perceptual re-alignment model. Specifically,
492 the visuo-centric hypothesis would predict that transient disruption of proprioception induced peripherally
493 by muscle vibration (46, 47) or centrally through non-invasive brain stimulation (48–51) would have no
494 impact on implicit adaptation. In contrast, assuming that reweighting is a gradual process, the perceptual
495 re-alignment model predicts that transient disruption of proprioception would heighten implicit
496 adaptation. Furthermore, using fMRI, the perceptual re-alignment model predicts that deafferented

497 participants, compared to controls, would exhibit less activation in brain areas conveying proprioceptive
498 information (e.g., the primary somatosensory cortex) and more activation in brain areas conveying
499 efferent-based sensory predictions (e.g., the cerebellum) and visual information (e.g., primary visual
500 cortex) throughout implicit adaptation.

501
502 *Study limitations*

503
504 While we have recruited one of the largest cohorts of rare deafferented participants to examine the effect
505 of proprioceptive loss on implicit adaptation (previous studies consist of case studies), the results remain
506 limited by the small sample size. Future studies could explore whether implicit adaptation is impacted in
507 patients with more prevalent forms of neuropathy, such as those induced by chemotherapy or diabetes,
508 although such conditions tend to produce less severe forms of proprioceptive loss. A larger sample would
509 provide a more robust means to evaluate not only whether proprioceptive impairment modulates
510 adaptation but also provide a means to ask about modulating variables such as the duration of
511 deafferentation.

512
513 We failed to find heightened perceived movement errors in deafferented adults. There are at least two
514 potential explanations for this null result. First, although the deafferentation was severe, the proximal
515 muscles of the upper extremity were possibly spared in a subset of our participants. As such, residual
516 proprioceptive input might have limited the magnitude of the perceived error. Future studies should
517 employ careful experimental designs and detailed kinematic analyses to ensure that the task relies solely
518 on the wrist and elbow movements as well as provide a more thorough characterization of participants'
519 deafferentation.

520
521 Second, participants might have used peripheral vision of their actual hand position, and such visual input
522 could impact both adaptation and perceptual reports. We conducted this study during the global pandemic
523 which prevented us from being physically present. We considered asking the participants to perform the
524 task without direct vision of the hand but based on our combined experience working with deafferented
525 patients (20, 21, 26), we anticipated that participants would struggle to return to the start position without
526 seeing their hand, potentially making the task frustrating. Empirically, this concern could be addressed in
527 future experiments in a controlled lab setting where we could occlude vision of the hand and passively
528 assist participants in returning to the start position with a robotic manipulandum (21, 24, 42).

529
530 While peripheral vision may be crucial for some aspects of motor control (52–55), prior literature
531 suggests that it does not play a major role in sensorimotor adaptation (56, 57). First, participants tend to
532 focus on the visual target throughout the movement rather than on their hand position during motor
533 adaptation (57–63). Second, movement kinematics, such as movement time and variability, appear
534 unaffected by the visibility of the hand (64, 65), implying that peripheral visual information about one's
535 hand position may not be critical for generating a feedforward motor plan. Third, our online results with
536 peripheral vision available align closely with in-lab results where peripheral vision was not possible (36,
537 66). Nonetheless, we cannot rule out the possibility that individuals used peripheral vision in the present
538 study. Future studies incorporating eye-tracking technology would be instrumental in determining the
539 extent to which peripheral vision is utilized by both deafferented and control groups.

540
541 Moreover, while there are notable kinematic differences between using a mouse and a trackpad (67, 68),
542 we do not believe that our results were substantially affected by the use of different computer devices.
543 Specifically, in a dataset comprising 2,000 individuals who were tested with our home-based on-line
544 platform, we did not observe significant differences in implicit adaptation between those who used
545 trackpad and those who used a mouse (36, 66). The results of this study and others using the on-line
546 platform suggest that the present results are unlikely to be affected because of our remote testing method.
547 We (69, 70) as well as other labs (71–74) have successfully replicated many classic adaptation

548 phenomena by conducting studies remotely. Therefore, this method offers the unique advantage of
549 conducting sensorimotor experiments with deafferented participants, or more generally, participants with
550 movement disorders, who may find it difficult and inconvenient to travel to a lab setting, especially when
551 there are constraints on in-person data collection (i.e., the COVID global pandemic).

552
553 In previous studies involving reports of perceived movement outcome during adaptation, the perceived
554 error reached a maximum value shortly after the onset of the visual perturbation and then dissipated over
555 time, returning to baseline levels in the last phase of adaptation (29, 75). Although this pattern was
556 evident in the mean data for the control participants, there was no statistical reduction in the perceived
557 movement error between the early and late adaptation phases. Several factors might account for this
558 observation: First, the study's duration may have been too short. Specifically, our experiment spanned 1.5
559 hours and consisted of 440 trials. This design choice was made to minimize fatigue and cater to the
560 mobility challenges faced by the deafferented participants. Extending the number of learning trials and
561 perceptual probes may clarify whether the perceived error diminishes as implicit adaptation ceases.

562
563 Second, the perceptual probes in our study may have been subject to unaccounted influences such as gaze
564 direction (76), transformations across horizontal and vertical workspaces, participants' interpretations of
565 the directive to "ignore the visual cursor", and the presence of a visual target. That is, participants, both
566 controls and patients, might have been inclined to base their perceptual reports on the location of the
567 visual target and clamped visual feedback, rather than on efferent and/or proprioceptive feedback
568 conveying hand position. To obtain a more precise measure, future studies could examine perceived
569 movement outcome after a passive or self-initiated movement, in the absence of both a visual cursor and
570 target (77).

571
572 *Conclusion*

573
574 Our findings indicate that chronic proprioceptive loss has minimal impact on implicit motor adaptation
575 and perceived movement outcome, posing a challenge for theoretical models of adaptation that involve
576 proprioception.

577 **References**

- 578
- 579 1. **Huberdeau DM, Krakauer JW, Haith AM.** Dual-process decomposition in human sensorimotor
580 adaptation. *Curr Opin Neurobiol* 33: 71–77, 2015.
- 581 2. **McDougle SD, Ivry RB, Taylor JA.** Taking Aim at the Cognitive Side of Learning in
582 Sensorimotor Adaptation Tasks. *Trends Cogn Sci* 20: 535–544, 2016.
- 583 3. **Tsay JS, Kim HE, McDougle SD, Taylor J, Haith A, Avraham G, Krakauer JW, Collins A,**
584 **Ivry R.** Fundamental processes in sensorimotor learning: Reasoning, Refinement, and Retrieval.
585 2023.
- 586 4. **Kim HE, Avraham G, Ivry RB.** The Psychology of Reaching: Action Selection, Movement
587 Implementation, and Sensorimotor Learning. .
- 588 5. **Zhang Z, Wang H, Zhang T, Nie Z, Wei K.** Perceptual error based on Bayesian cue combination
589 drives implicit motor adaptation. *bioRxiv*: 2023.11.23.568442, 2023.
- 590 6. **Tsay JS, Kim H, Haith AM, Ivry RB.** Understanding implicit sensorimotor adaptation as a process
591 of proprioceptive re-alignment. *Elife* 11, 2022. doi: 10.7554/eLife.76639.
- 592 7. **Wolpert DM, Ghahramani Z, Jordan MI.** An internal model for sensorimotor integration. *Science*
593 269: 1880–1882, 1995.
- 594 8. **Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL.** Motor commands contribute to
595 human position sense. *J Physiol* 571: 703–710, 2006.
- 596 9. **Desmurget M, Grafton S.** Forward modeling allows feedback control for fast reaching movements.
597 *Trends Cogn Sci* 4: 423–431, 2000.
- 598 10. **Proske U, Gandevia SC.** The proprioceptive senses: their roles in signaling body shape, body
599 position and movement, and muscle force. *Physiol Rev* 92: 1651–1697, 2012.
- 600 11. **Ernst MO, Di Luca M.** Multisensory Perception: From Integration to Remapping. *Sensory Cue*
601 *Integration*: 224–250, 2011.
- 602 12. **Bhanpuri NH, Okamura AM, Bastian AJ.** Predictive modeling by the cerebellum improves
603 proprioception. *J Neurosci* 33: 14301–14306, 2013.
- 604 13. **Sober SJ, Sabes PN.** Multisensory integration during motor planning. *J Neurosci* 23: 6982–6992,
605 2003.
- 606 14. **Rossi C, Bastian AJ, Therrien AS.** Mechanisms of proprioceptive realignment in human motor
607 learning. *Current Opinion in Physiology* 20: 186–197, 2021.
- 608 15. **Fassold ME, Locke SM, Landy MS.** Feeling lucky? Prospective and retrospective cues for
609 sensorimotor confidence. *PLoS Comput Biol* 19: e1010740, 2023.
- 610 16. **Rothwell JC, Traub MM, Day BL, Obeso JA, Thomas PK, Marsden CD.** Manual motor
611 performance in deafferented man. *Brain* 105: 515–542, 1982.

- 612 17. **Sterman AB, Schaumburg HH, Asbury AK.** The acute sensory neuronopathy syndrome: a distinct
613 clinical entity. *Ann Neurol* 7: 354–358, 1980.
- 614 18. **Cole J, Sedgwick EM.** The perceptions of force and of movement in a man without large
615 myelinated sensory afferents below the neck. *J Physiol* 449: 503–515, 1992.
- 616 19. **Chesler AT, Szczot M, Bharucha-Goebel D, Āeko M, Donkervoort S, Laubacher C, Hayes LH,**
617 **Alter K, Zampieri C, Stanley C, Innes AM, Mah JK, Grosmann CM, Bradley N, Nguyen D,**
618 **Foley AR, Le Pichon CE, Bönemann CG.** The role of PIEZO2 in human mechanosensation. *N*
619 *Engl J Med* 375: 1355–1364, 2016.
- 620 20. **Bernier P-M, Chua R, Bard C, Franks IM.** Updating of an internal model without proprioception:
621 a deafferentation study. *Neuroreport* 17: 1421–1425, 2006.
- 622 21. **Miall RC, Kitchen NM, Nam S-H, Lefumat H, Renault AG, Ørstavik K, Cole JD, Sarlegna**
623 **FR.** Proprioceptive loss and the perception, control and learning of arm movements in humans:
624 evidence from sensory neuronopathy. *Exp Brain Res* 236: 2137–2155, 2018.
- 625 22. **Miller LE, Fabio C, Ravenda V, Bahmad S, Koun E, Salemme R, Luauté J, Bolognini N,**
626 **Hayward V, Farnè A.** Somatosensory cortex efficiently processes touch located beyond the body.
627 *Curr Biol* 29: 4276-4283.e5, 2019.
- 628 23. **Sarlegna FR, Sainburg RL.** The roles of vision and proprioception in the planning of reaching
629 movements. *Adv Exp Med Biol* 629: 317–335, 2009.
- 630 24. **Yousif N, Cole J, Rothwell J, Diedrichsen J.** Proprioception in motor learning: lessons from a
631 deafferented subject. *Exp Brain Res* 233: 2449–2459, 2015.
- 632 25. **Ingram HA, van Donkelaar P, Cole J, Vercher JL, Gauthier GM, Miall RC.** The role of
633 proprioception and attention in a visuomotor adaptation task. *Exp Brain Res* 132: 114–126, 2000.
- 634 26. **Sarlegna FR, Malfait N, Bringoux L, Bourdin C, Vercher J-L.** Force-field adaptation without
635 proprioception: can vision be used to model limb dynamics? *Neuropsychologia* 48: 60–67, 2010.
- 636 27. **Lefumat HZ, Miall RC, Cole JD, Bringoux L, Bourdin C, Vercher J-L, Sarlegna FR.**
637 Generalization of force-field adaptation in proprioceptively-deafferented subjects. *Neurosci Lett*
638 616: 160–165, 2016.
- 639 28. **Tsay JS, Kim HE, McDougle SD, Taylor J, Haith A, Avraham G, Krakauer JW, Collins A,**
640 **Ivry R.** Strategic Processes in Sensorimotor Learning: Reasoning, Refinement, and Retrieval
641 [Online]. 2023. psyarxiv.com/x4652.
- 642 29. **Tsay JS, Parvin DE, Ivry RB.** Continuous reports of sensed hand position during sensorimotor
643 adaptation. *J Neurophysiol* 124: 1122–1130, 2020.
- 644 30. **Morehead R, Taylor JA, Parvin DE, Ivry RB.** Characteristics of Implicit Sensorimotor
645 Adaptation Revealed by Task-irrelevant Clamped Feedback. *J Cogn Neurosci* 29: 1061–1074, 2017.
- 646 31. **Lin S-H, Cheng Y-R, Banks RW, Min M-Y, Bewick GS, Chen C-C.** Evidence for the
647 involvement of ASIC3 in sensory mechanotransduction in proprioceptors. *Nat Commun* 7: 11460,
648 2016.

- 649 32. **Cole J, Katifi HA.** Evoked potentials in a man with a complete large myelinated fibre sensory
650 neuropathy below the neck. *Evok Pot* 80: 103–107, 1991.
- 651 33. **Miall RC, Rosenthal O, Ørstavik K, Cole JD, Sarlegna FR.** Loss of haptic feedback impairs
652 control of hand posture: a study in chronically deafferented individuals when grasping and lifting
653 objects. *Exp Brain Res* 237: 2167–2184, 2019.
- 654 34. **Cardinali L, Brozzoli C, Luauté J, Roy AC, Farnè A.** Proprioception Is Necessary for Body
655 Schema Plasticity: Evidence from a Deafferented Patient. *Front Hum Neurosci* 10: 272, 2016.
- 656 35. **Schaffer JE, Sarlegna FR, Sainburg RL.** A rare case of deafferentation reveals an essential role of
657 proprioception in bilateral coordination. *Neuropsychologia* 160: 107969, 2021.
- 658 36. **Tsay JS, Lee A, Ivry RB, Avraham G.** Moving outside the lab: The viability of conducting
659 sensorimotor learning studies online [Online]. <http://arxiv.org/abs/2107.13408>.
- 660 37. **Sassenhagen J, Draschkow D.** Cluster-based permutation tests of MEG/EEG data do not establish
661 significance of effect latency or location. *Psychophysiology* 56: e13335, 2019.
- 662 38. **Chen Y, Abram SJ, Ivry RB, Tsay JS.** Motor adaptation is reduced by symbolic compared to
663 sensory feedback. *bioRxiv*: 2024.06.28.601293, 2024.
- 664 39. **Burge J, Ernst MO, Banks MS.** The statistical determinants of adaptation rate in human reaching.
665 *J Vis* 8: 20.1–19, 2008.
- 666 40. **Tsay JS, Kim HE, Parvin DE, Stover AR, Ivry RB.** Individual differences in proprioception
667 predict the extent of implicit sensorimotor adaptation. .
- 668 41. **Salomonczyk D, Cressman EK, Henriques DYP.** The role of the cross-sensory error signal in
669 visuomotor adaptation. *Exp Brain Res* 228: 313–325, 2013.
- 670 42. **Ostry DJ, Darainy M, Mattar AAG, Wong J, Gribble PL.** Somatosensory plasticity and motor
671 learning. *J Neurosci* 30: 5384–5393, 2010.
- 672 43. **Bard C, Turrell Y, Fleury M, Teasdale N, Lamarre Y, Martin O.** Deafferentation and pointing
673 with visual double-step perturbations. *Exp Brain Res* 125: 410–416, 1999.
- 674 44. **Fleury M, Bard C, Teasdale N, Paillard J, Cole J, Lajoie Y, Lamarre Y.** Weight judgment.
675 *Brain* 118: 1149–1156, 1995.
- 676 45. **Sarlegna FR, Gauthier GM, Bourdin C, Vercher J-L, Blouin J.** Internally driven control of
677 reaching movements: a study on a proprioceptively deafferented subject. *Brain Res Bull* 69: 404–
678 415, 2006.
- 679 46. **Goodwin GM, McCloskey DI, Matthews PB.** Proprioceptive illusions induced by muscle
680 vibration: contribution by muscle spindles to perception? *Science* 175: 1382–1384, 1972.
- 681 47. **Eschelmuller G, Chua R, Carpenter MG, Inglis JT.** The acute effects of periodic and noisy
682 tendon vibration on wrist muscle stretch responses. *Neurosci Lett* 764: 136279, 2021.
- 683 48. **Kumar N, Manning TF, Ostry DJ.** Somatosensory cortex participates in the consolidation of
684 human motor memory. *PLoS Biol* 17: e3000469, 2019.

- 685 49. **Ohashi H, Gribble PL, Ostry DJ.** Somatosensory cortical excitability changes precede those in
686 motor cortex during human motor learning. *J Neurophysiol* 122: 1397–1405, 2019.
- 687 50. **Ebrahimi S, Ostry DJ.** The human somatosensory cortex contributes to the encoding of newly
688 learned movements. *Proc Natl Acad Sci U S A* 121: e2316294121, 2024.
- 689 51. **Mirdamadi JL, Block HJ.** Somatosensory versus cerebellar contributions to proprioceptive
690 changes associated with motor skill learning: A theta burst stimulation study [Online].
691 <https://www.biorxiv.org/content/10.1101/2020.08.06.239707v1.full.pdf>.
- 692 52. **Blouin J, Teasdale N, Bard C, Fleury M.** Directional control of rapid arm movements: the role of
693 the kinetic visual feedback system. *Can J Exp Psychol* 47: 678–696, 1993.
- 694 53. **Gouirand N, Mathew J, Brenner E, Danion FR.** Eye movements do not play an important role in
695 the adaptation of hand tracking to a visuomotor rotation. *J Neurophysiol* 121: 1967–1976, 2019.
- 696 54. **Paillard J.** Fast and slow feedback loops for the visual correction of spatial errors in a pointing task:
697 a reappraisal. *Can J Physiol Pharmacol* 74: 401–417, 1996.
- 698 55. **Sarlegna F, Blouin J, Vercher J-L, Bresciani J-P, Bourdin C, Gauthier GM.** Online control of
699 the direction of rapid reaching movements. *Exp Brain Res* 157: 468–471, 2004.
- 700 56. **Grigorova V, Bock O.** The role of eye movements in visuo-manual adaptation. *Exp Brain Res* 171:
701 524–529, 2006.
- 702 57. **de Brouwer AJ, Albaghdadi M, Flanagan JR, Gallivan JP.** Using gaze behavior to parcellate the
703 explicit and implicit contributions to visuomotor learning. *J Neurophysiol* 120: 1602–1615, 2018.
- 704 58. **Rand MK, Rentsch S.** Gaze locations affect explicit process but not implicit process during
705 visuomotor adaptation. *J Neurophysiol* 113: 88–99, 2015.
- 706 59. **Paillard SF.** The contribution of peripheral and central vision to visually guided reaching. In:
707 *Analysis of Visual Behaviour*, edited by Ingle DJ. MIT Press, 1982, p. 367–385.
- 708 60. **Baldauf D, Wolf M, Deubel H.** Deployment of visual attention before sequences of goal-directed
709 hand movements. *Vision Res* 46: 4355–4374, 2006.
- 710 61. **Abrams RA, Meyer DE, Kornblum S.** Eye-hand coordination: Oculomotor control in rapid aimed
711 limb movements. *J Exp Psychol Hum Percept Perform* 16: 248–267, 1990.
- 712 62. **Bromberg Z, Donchin O, Haar S.** Eye movements during visuomotor adaptation represent only
713 part of the explicit learning. *bioRxiv*: 724864, 2019.
- 714 63. **Abekawa N, Ito S, Gomi H.** Gaze-specific motor memories for hand-reaching. *Curr Biol* 32: 2747-
715 2753.e6, 2022.
- 716 64. **Prablanc C, Echallier JE, Jeannerod M, Komilis E.** Optimal response of eye and hand motor
717 systems in pointing at a visual target. II. Static and dynamic visual cues in the control of hand
718 movement. *Biol Cybern* 35: 183–187, 1979.
- 719 65. **Goodale MA, Pelisson D, Prablanc C.** Large adjustments in visually guided reaching do not
720 depend on vision of the hand or perception of target displacement. *Nature* 320: 748–750, 1986.

- 721 66. **Tsay JS, Asmerian H, Germine LT, Wilmer J, Ivry RB, Nakayama K.** Large-scale citizen
722 science reveals predictors of sensorimotor adaptation. .
- 723 67. **Sako S, Sugiura H, Tanoue H, Kojima M, Kono M, Inaba R.** Electromyographic analysis of
724 relevant muscle groups during completion of computer tasks using different computer mouse
725 positions. *Int J Occup Saf Ergon* 23: 267–273, 2017.
- 726 68. **Conte C, Ranavolo A, Serrao M, Silvetti A, Orenco G, Mari S, Forzano F, Iavicoli S,
727 Draicchio F.** Kinematic and electromyographic differences between mouse and touchpad use on
728 laptop computers. *Int J Ind Ergon* 44: 413–420, 2014.
- 729 69. **Wang T, Avraham G, Tsay JS, Abram SJ, Ivry RB.** Perturbation variability does not influence
730 implicit sensorimotor adaptation. *PLoS Comput Biol* 20: e1011951, 2024.
- 731 70. **Tsay JS, Haith AM, Ivry RB, Kim HE.** Interactions between sensory prediction error and task
732 error during implicit motor learning. *PLoS Comput Biol* 18: e1010005, 2022.
- 733 71. **Shyr MC, Joshi SS.** A case study of the validity of web-based visuomotor rotation experiments. .
- 734 72. **Jang J, Shadmehr R, Albert ST.** A software tool for at-home measurement of sensorimotor
735 adaptation. *bioRxiv*: 2023.12.12.571359, 2023.
- 736 73. **Watral A.** Assessing the validity of an online assessment of motor learning. Michigan
737 Technological University: 2022.
- 738 74. **Kim OA, Forrence AD, McDougle SD.** Motor learning without movement. *Proc Natl Acad Sci U S
739 A* 119: e2204379119, 2022.
- 740 75. **Synofzik M, Thier P, Lindner A.** Internalizing agency of self-action: perception of one’s own hand
741 movements depends on an adaptable prediction about the sensory action outcome. *J Neurophysiol*
742 96: 1592–1601, 2006.
- 743 76. **Jones SAH, Henriques DYP.** Memory for proprioceptive and multisensory targets is partially
744 coded relative to gaze. *Neuropsychologia* 48: 3782–3792, 2010.
- 745 77. **Izawa J, Shadmehr R.** Learning from sensory and reward prediction errors during motor
746 adaptation. *PLoS Comput Biol* 7: e1002012, 2011.