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Implicit motor adaptation and perceived hand position without proprioception: A kinesthetic error may be derived from efferent signals

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Abstract

Our ability to produce successful goal-directed actions involves multiple learning processes. Among these, implicit adaptation is of utmost importance, keeping our sensorimotor system well-calibrated in response to changes in the body and environment. Implicit adaptation is assumed to be driven by a sensory prediction error, the difference between the predicted and actual sensory consequences of a movement. Whereas most models of implicit adaptation have focused on how visual information defines the sensory prediction error, we have recently proposed that this error signal is kinesthetic, the difference between the desired and perceived hand position, with adaptation serving to align these two signals and restore optimal motor performance (Tsay et al., 2022). Here, we examined implicit adaptation and kinesthetic perception in rare individuals who lack proprioceptive signals from the upper limbs. We used a visuomotor rotation task designed to isolate implicit adaptation while simultaneously probing the participants' perceived hand position. Consistent with prior work, control participants exhibited robust implicit adaptation and the signature of kinesthetic re-alignment, an initial bias in perceived hand position towards the visual cursor and a gradual shift back to the movement goal. Strikingly, the time course of both implicit adaptation and kinesthetic re-alignment was preserved in the deafferented group, suggesting that proprioceptive afferents are not necessary for implicit adaptation and kinesthetic re-alignment. We propose that a kinesthetic prediction error derived from efferent motor signals is sufficient to drive implicit adaptation and to re-algin a biased percept of hand position with the movement goal.

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Introduction

Multiple learning processes operate to ensure that motor performance remains successful in the face of changes in the environment and body. 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. This latter process is thought to be driven by a sensory prediction error, the difference between the predicted and the actual sensory feedback (Rossi et al., 2021; Shadmehr et al., 2010; Daniel M. Wolpert et al., 2011).

Current models of implicit sensorimotor adaptation are either agnostic regarding the sources of information for the sensory prediction and feedback, or have focused on how vision defines the target goal and provides the critical source of feedback (Albert et al., 2022, 2021; Donchin et al., 2003; Herzfeld et al., 2014; Kim et al., 2018; Morehead & Smith, 2017; Thoroughman & Shadmehr, 2000). By this visuo-centric view, implicit adaptation is an iterative process designed to minimize a visual sensory prediction error, with the extent of implicit adaptation representing a point of equilibrium: Performance will asymptote when the trial-by-trial change in the sensorimotor map in response to the visual sensory prediction error is counterbalanced by trial-by-trial decay of this map back towards its baseline, default state (Morehead & Smith, 2017).

Despite its appeal, the visuo-centric view fails to capture key features of implicit sensorimotor adaptation. On ecological grounds, the ultimate purpose of reaching is to move the hand to a desired position (e.g., grasp an object), with success determined by an alignment of the desired and perceived hand position. The sensorimotor system exploits multiple cues to build a unified percept of hand position, what we refer to in the present article as the kinesthetic percept (Cole & Sedgwick, 1992; Sarlegna & Sainburg, 2009; Smeets et al., 2006; Sober & Sabes, 2005; van der Kooij et al., 2013). These cues include proprioceptive (Cole, 1991; Inglis & Frank, 1990; Rothwell et al., 1982), tactile (Edin & Johansson, 1995), and visual inputs (Burge et al., 2008; Ferrea et al., 2021), as well as cross-model interactions (Cressman et al., 2010; Ernst & Banks, 2002) between these afferent sources. In addition, the composite kinesthetic signal is influenced by non-sensory information like prior beliefs about the desired movement outcome (Fassold et al., 2022; Körding & Wolpert, 2004). As such, when the action falls short of the goal – the cup is missed or improperly grasped – the sensorimotor system is likely to exploit multiple sources of information in defining the sensory prediction error that drives adaptation.

These insights led us to propose a 'kinesthetic re-alignment' model of implicit adaptation. (Footnote: In the original exposition of this model (Tsay, Kim, et al., 2022), we used the phrase "proprioceptive re-alignment." However, we will adopt the term "kinesthetic" here given that this better captures the idea that the perceived position of the hand is an integrated signal comprised of multisensory and predictive inputs derived from efferent signals (Proske & Gandevia, 2012)). In this model, implicit adaptation is conceptualized as an iterative process designed to minimize a kinesthetic prediction error, the difference between the desired and perceived hand position. Consider what happens when a visual perturbation is introduced in an upper-limb reaching task. Due to multisensory integration, the perceived hand position will be biased away from the movement goal towards the visual cursor, with this shift introducing a kinesthetic error. This kinesthetic error drives participants to adapt by moving the hand in the opposite direction of the perturbed visual cursor. Implicit adaptation ceases when the perceived hand position is re-aligned with the movement goal.

Unlike visuo-centric models, the kinesthetic re-alignment model can account for implicit adaptation even in the absence of visual feedback (Franklin et al., 2007; Lackner & Dizio, 1994; Lefumat et al., 2016), as well as correlations between the magnitude and variability of biases in perceived hand position and implicit adaptation (Tsay, Kim, et al., 2021). Moreover, the model accounts for the dynamics of the participants'

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phenomenal experience of perceived hand position. In one study, we used a visuomotor task that isolates implicit adaptation and probed the participants' perceived hand position over the course of adaptation (Tsay et al., 2020) (also see: (Synofzik et al., 2010)). At asymptote, the actual change in hand position was around 20°. However, the participants reported that their hand was close to the target location, confirming that participants were unaware of their adapted state. Moreover, the kinesthetic reports revealed an intriguing pattern: Initially, the participants perceived their hand to be biased towards the perturbed visual feedback. Over the course of adaptation, the reports gradually shifted away from the perturbed visual feedback, eventually converging with the movement goal (i.e., the visual target). We assume that the initial shift towards the perturbed visual feedback introduced a kinesthetic error and that adaptation reached an asymptote when this error was nullified, that is, when kinesthetic re-alignment has been achieved. These systematic changes in perceived hand position cannot be accounted for by visuo-centric models of implicit adaptation.

Individuals who lack proprioceptive and tactile inputs from the upper limb present an interesting test case for models of implicit adaptation. 'Deafferentation' is a rare condition that can arise from a congenital disorder or a neurological insult (Bernier et al., 2006; Chesler et al., 2016; Cole & Sedgwick, 1992; Miall et al., 2018; Miller et al., 2019; Rothwell et al., 1982; Sarlegna & Sainburg, 2009; Sterman et al., 1980). While previous case studies have observed preserved adaptation in deafferented adults (Bernier et al., 2006; Ingram et al., 2000; Lefumat et al., 2016; Miall et al., 2018; Sarlegna et al., 2010; Yousif et al., 2015), the tasks used in these studies have not isolated implicit adaptation. Even if one assumes that the adaptation was implicit, both visuo-centric and kinesthetic re-alignment models can account for the results. Consider the situation when the perturbation involves a standard visuomotor rotation: By the visuo-centric model, implicit adaptation is driven by a visual sensory prediction error that arises from the visual perturbation; by the kinesthetic re-alignment model, implicit adaptation is driven by a kinesthetic prediction error that arises when the visual perturbation induces a shift in perceived hand position. Since visual feedback is contingent on hand position, both models predict that implicit adaptation will cease when the visual feedback is aligned with the target (eliminating both visual and kinesthetic prediction errors).

To arbitrate between the two models of implicit adaptation, we tested a cohort of deafferented individuals on a modified visuomotor rotation task that isolates implicit adaptation and allows us to intermittently probe perceived hand position (Morehead et al., 2017; Tsay et al., 2020). Unlike standard adaptation tasks in which the position of the feedback is contingent on the position of the hand, participants experienced a fixed visual perturbation ("clamped feedback"), one that is independent of hand position. By the visuo-centric model, we would expect normal implicit adaptation in deafferented individuals: The visual sensory prediction error will drive implicit adaptation, reaching asymptote when the trial-by-trial change in heading direction is counterbalanced by forgetting. Moreover, the deafferented participants should not exhibit signatures of kinesthetic re-alignment, always perceiving their hand near the movement goal. (Footnote: Given that visuo-centric models do not reference the perceived hand position, it is not clear what these models predict in terms of kinesthetic experience. We highlight here that the percept will be near the target given that this is the implicit assumption for participants with normal afference and return to this issue in the Discussion.)

In contrast, by the kinesthetic re-alignment model, we might expect heightened implicit adaptation in the deafferented group. Unlike controls whose perceived hand is a composite of proprioceptive and visual inputs, along with a prior related to the desired sensory outcome (i.e., the target), only the latter two sources provide information for perceived hand position in individuals with deafferentation since the critical proprioceptive inputs are absent (or very severely weakened). As such, implicit adaptation would be heightened in deafferented participants attempting to offset the kinesthetic bias towards the visual perturbation. Correspondingly, deafferented participants should also exhibit the key signature of kinesthetic re-alignment, that is, an initial bias in perceived hand position towards the visual cursor and a gradual shift back to the movement goal.

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Results

Implicit adaptation is preserved but not heightened in deafferented individuals

We compared the performance of six deafferented participants with their matched controls on a visuomotor rotation task. Our task differed from prior studies of adaptation in this population in two notable ways. First, given that deafferentation was less complete in proximal muscles of our participants, our task involved "reaches" that were limited to movements about the wrist and/or fingers. Second, we used clamped visual feedback, a method that isolates implicit adaptation and provides a measure of the upper bound of adaptation that is independent of the error size (Morehead et al., 2017) (Figure 1A). In this task, participants reach to a visual target and receive cursor visual feedback that follows a fixed trajectory defined relative to the target. Thus, unlike standard perturbation methods, the angular position of the feedback is not contingent on the participant's movement direction. (Note that the radial position of the cursor is linked to the participant's movement.) Participants are fully informed of this manipulation and instructed to always reach directly to the target while ignoring the visual feedback. Despite these instructions, the visual perturbation between the position of the target and the cursor elicits an implicit adaptive response, causing a change in movement direction away from the target and in the opposite direction to the cursor. Interestingly, across a large range of clamp angles, adaptation saturates at a common value, averaging between 20° and 30° across healthy participants (Kim et al., 2018; Morehead et al., 2017). These motor adjustments are not the result of explicit re-aiming; indeed, participants are oblivious to the change in their behavior (Tsay et al., 2020).

Consistent with previous studies using the clamped feedback task, the control group showed a gradual change in hand angle in the opposite direction of the 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 adaptation. These data provide a compelling demonstration that implicit adaptation is preserved despite the loss of proprioceptive and tactile afferents.

We analyzed the data at three phases in the experiment, with each measure calculated relative to the participant's idiosyncratic baseline bias: Early adaptation, late adaptation, and aftereffect phases. Robust implicit adaptation was observed during all three phases of the experiment for both groups (all phases vs baseline hand angle, $t(192) > 4.6, p < 0.001, D > 1.9$). Notably, all of the deafferented participants showed a significant aftereffect (vs baseline: IW: $t(9) = 12.3, p < 0.001, D_z = 3.9$; CM: $t(9) = 13.6, p < 0.001, D_z = 4.3$; CD: $t(9) = 6.5, p < 0.001, D_z = 2.1$; SB: $t(9) = 5.2, p < 0.001, D_z = 1.6$; DC: $t(9) = 15.6, p < 0.001, D_z = 4.9$; WL: $t(9) = 8.8, p < 0.001, D_z = 2.8$).

There was a main effect of phase ($F(2, 128) = 169, p < 0.001, \eta^2 = 0.44$) with the change in hand angle increasing from early to late adaptation ($t(192) = 9.3, p < 0.001, D_z = 1.1$). Because we limited the number of trials to avoid fatiguing the deafferented participants, it is unclear if adaptation had reached asymptote by the end of the clamped feedback block. Nonetheless, the group averaged functions appear to be approaching asymptote. To assess this on an individual basis, we compared fits of the data for each individual with either a linear or non-linear asymptotic function (i.e., Michaelis–Menten saturation curve, (Michaelis & Menten, 1913)). All of the individual functions were better fit with the non-linear asymptotic function (average mean squared error ± SD: linear, 0.11° ± 0.07°; saturated: 0.05° ± 0.04°; $t(64) = 6.5, p < 0.001, D_z = 0.8$). During the aftereffect block when the visual feedback was eliminated, hand angle remained at a similar value to that observed late in adaptation (late adaption vs aftereffects: $t(192) = -1.2, p = 0.45, D_z = 0.1$). This latter result highlights that the changes in hand angle elicited by clamped feedback are implicit.

Turning to our main question, we did not observe any differences in the rate and degree of implicit adaptation between the deafferented and control participants. There was neither a significant main effect of

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group ($F(1,98) = 021, p = 0.64, \eta^2 = 0.00, BF_{01} = 3.9$, moderate evidence for the null) nor a significant interaction between group and phase ($F(2,128) = 1.0, p = 0.38, \eta^2 = 0.02, BF_{01} = 3.4$, moderate evidence for the null). These results underscore that implicit adaptation is preserved in deafferented individuals. However, the null results indicate that this condition does not result in heightened adaptation.

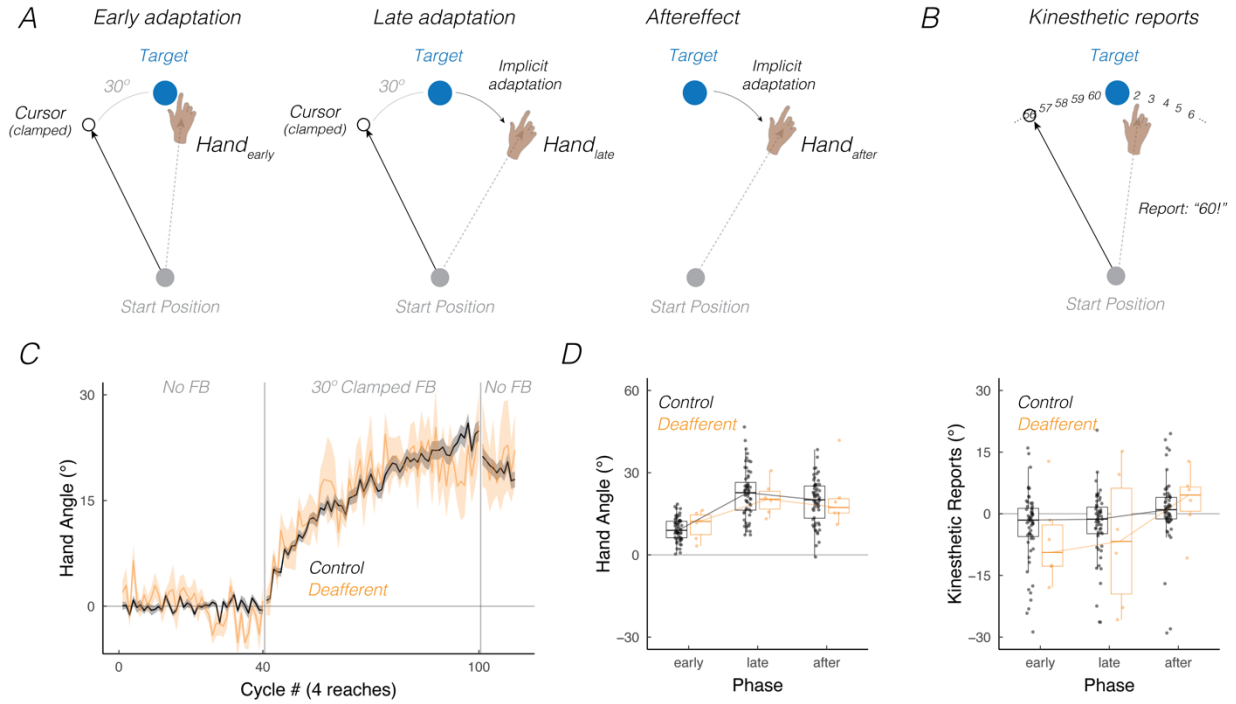

Figure 1: Implicit adaptation and pattern of kinesthetic errors are preserved in individuals with deafferentation. (A) Schematic of the visual clamped feedback task. After baseline trials without cursor feedback (cycles 1 – 40), participants were exposed to 240 trials with clamped visual feedback (cycles 41 – 100) in which the cursor (white circle) followed a fixed trajectory, rotated 30° counterclockwise relative to the target. Participants were instructed to always move directly to the target (blue circle) and ignore the visual clamped feedback. Left, middle and right panels are schematics of hand 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 report their perceived hand position. 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 panel). 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 where they perceived their hand had been when reaching the target distance. Kinesthetic reports during early, late and aftereffect phases (bottom panel); negative and positive kinesthetic reports denote perceived hand position towards or away from the cursor, respectively. **(C)** Mean time courses of hand angle for Control (black; N = 60) and Deafferented groups (orange; N = 6). Shaded areas represent standard error. Hand angle is presented relative to the target (0°); negative and positive hand angles denote movements towards or away from the cursor, respectively. One cycle consisted of four movements, one to each of the four possible target locations. **(D)** Summary of implicit adaptation (left) and hand report data (right) for the three learning probes. The adaptation values were calculated relative to each participant's baseline bias. Box plots show minimum, median, maximum, and 1st/3rd interquartile values. Dots denote individuals.

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Pattern of kinesthetic errors is preserved in deafferented individuals

We next turned to the question of how adaptation influenced perceived hand position in the two groups. Periodically during the task, participants were asked to report their perceived hand position (Figure 1B, top). Specifically, every 10th movement cycle, a number wheel appeared on the screen immediately after the center-out movement was completed (i.e., one report provided following a reach to each of the four targets). The participant reported their perceived hand position when the hand crossed the target distance using the computer keyboard to type in the number closest to their perceived hand 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.

Consistent with prior work (Tsay et al., 2020), the hand position reports for the control participants exhibited systematic changes over the course of implicit adaptation: The participants initially perceived their hand to be biased towards the perturbed visual feedback (denoted by a negative reports in Figure 1B, bottom) and thus, mis-aligned with the target. The magnitude of this initial bias (~5°) towards the visual cursor is similar to that observed in prior work (Ruttle et al., 2021; Tsay et al., 2020). Over time the reports shifted away from the perturbed visual feedback, converging back to the target (denoted by near zero reports). The convergence in kinesthetic reports between in-lab and our current web-based approach is noteworthy in light of several methodological differences with our initial hand report task. In Tsay et al. (2020), the hand was completely occluded by a horizontal monitor and the number wheel was in the same plane as the reaching movement. Here, the number wheel was presented in an orthogonal plane, requiring a coordinate transformation. Moreover, vision of the hand was possible although informal observation indicated that participants remained focused on the screen given their attention to the target and number wheel (for similar methods, see (Rand & Heuer, 2019)). The fact that systematic biases in hand report were observed would suggest that these methodological changes did not impact the participants' phenomenal experience.

Strikingly, the hand report function for the deafferented group virtually overlaps the control function. Thus, even in the absence of proprioceptive feedback, the perception of hand position was modified, and importantly, followed the dynamics exhibited by control participants. Statistically, there was a main effect of phase ($F(2,128) = 5.3, p = 0.006, \eta^2 = 0.1$). During early adaptation, perceived hand position in both groups shifted towards the visual cursor ($t(65) = -3.2, p = 0.002, D_z = 0.4$). Over the course of adaptation, this initial bias dissipated, with the perceived hand position in the late adaptation and aftereffect phases converging near the target position ($t(65) = 1.2, p = 0.23, D_z = 0.1$). There was neither a significant main effect of Group ($F(1,177) = 0.6, p = 0.42, \eta^2 = 0.0$) nor a significant interaction between Group and Phase ($F(2,128) = 0.7, p = 0.51, \eta^2 = 0.01$). These results indicate that the signature of kinesthetic re-alignment is preserved in deafferented individuals.

(Footnote: We correlated the magnitude of the initial kinesthetic shift and extent of implicit adaptation across all individuals. While the correlation was in the direction observed in prior studies (Ruttle et al., 2021; Tsay, Kim, et al., 2021) – a greater kinesthetic shift generating a greater extent of implicit adaptation – the correlation was not significant ($R = 0.1, p = 0.67$). However, unlike our study in which the hand reports were obtained after a movement, the previous studies relied on a passive method to estimate the change in kinesthesia following the introduction of perturbation. Since passive displacement of the hand was not possible in our online study, the kinesthetic reports in early adaptation served as a coarse proxy for the initial kinesthetic shift shortly after the introduction of the clamped perturbation. With this method, the judgments are likely noisier due to the movement.)

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Motor control impairments in deafferented individuals

To evaluate whether motor control is impaired in deafferented individuals, we focused on the kinematic data from the baseline phase, prior to the introduction of the perturbed feedback. As shown in Figure 2, there were no significant group differences in movement time (Control: 102.0 ± 10.1 ms, Deafferent: 92.3 ± 12.3 ms; $t(14) = 0.6, p = 0.60, D = 0.1$). Moreover, neither group showed a significant bias in heading angle during the baseline block (baseline vs 0: Controls, $t(59) = -0.4, p = 0.69, D_z = 0.1$; Deafferent: $t(5) = -0.8, p = 0.46, D_z = 0.1$). However, hand angle variability was larger in the deafferented group compared to controls (Hand angle SD: Control: $6.4 \pm 0.4°$, Deafferent: $8.9 \pm 0.9°$; $t(7) = 2.7, p = 0.03, D = 0.9$), indicating that movements are less consistent when proprioception is impaired.

Given this difference, we repeated our between-group analysis of implicit adaptation included hand 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, implicit adaptation is preserved in deafferented adults despite their motor control impairment.

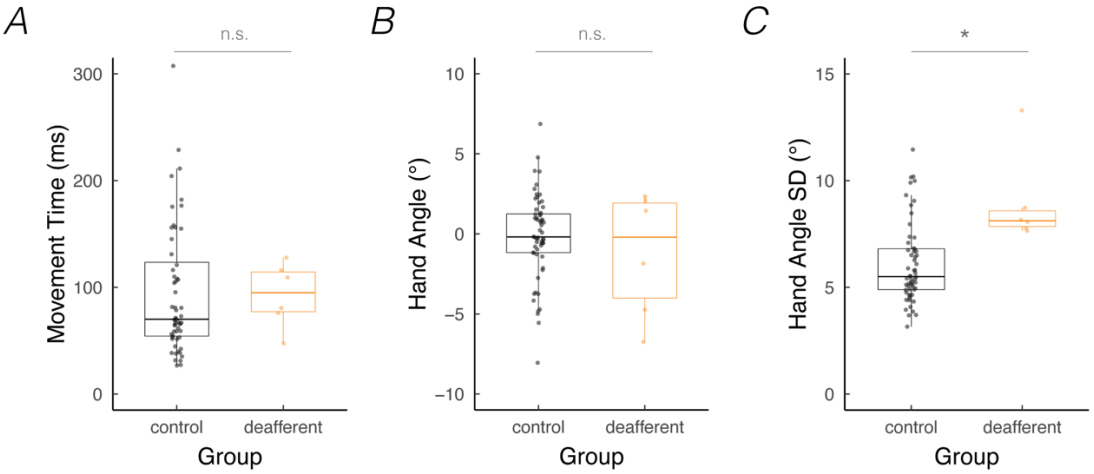

Figure 2: Deafferented individuals show deficits in movement consistency. (A) Movement time, **(B)** mean hand angle, and **(C)** hand angle variability during baseline no-feedback trials in deafferented individuals (orange) compared their matched controls (black). Box plots show minimum, median, maximum, and 1st/3rd interquartile values. Dots denote individuals. * denotes p<0.05.

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Discussion

Implicit adaptation ensures that the sensorimotor system remains exquisitely calibrated in response to changes in the body and environment. Mechanistically, implicit adaptation is thought to be driven by sensory prediction error, the difference between the predicted feedback associated with an efferent motor command and the actual sensory feedback (Rossi et al., 2021; Shadmehr et al., 2010; Daniel M. Wolpert et al., 2011). Traditionally, models of visuomotor adaptation have focused on how the target position, specified by vision, serves as a proxy of the prediction, and is compared with visual feedback in defining the sensory prediction error. However, motivated by limitations with a visuo-centric view, we have proposed an alternative kinesthetic re-alignment model, which reframes implicit adaptation as a process driven by a kinesthetic error, the mismatch between the perceived and desired position of the hand (Tsay et al., 2022). By this view, the perceived hand position is not just influenced by vision but also reflects information from proprioceptive afferents and prior beliefs about the desired sensory outcome (i.e., the target).

Previous neuropsychological work has shown that motor adaptation for reaching movements is preserved in individuals with upper limb impairment in proprioception and touch (Bernier et al., 2006). Superficially, this result seems to favor the visuocentric model, indicating that proprioceptive and tactile afferents are not necessary for implicit motor adaptation. However, the performance changes might have come about from other adaptation processes (e.g., explicit re-aiming) since the tasks did not isolate implicit adaptation. Moreover, even if one assumes that the adaptation was implicit, visuo-centric and kinesthetic re-alignment models can both account for the results.

To arbitrate between these two models of implicit adaptation, rare deafferented individuals were tested on a visuomotor rotation task that isolates implicit adaptation. Importantly, we also intermittently probed their perceived hand position, providing a critical measure to discriminate between the visuo-centric and kinesthetic re-alignment models. Indeed, we found that control participants exhibited robust implicit adaptation and concomitant signatures of kinesthetic re-alignment, that is, an initial bias in kinesthesia towards the visual cursor and a gradual return to the movement goal. Strikingly, the results on both measures were similar for the deafferented and control participants. They showed a similar rate and magnitude of adaptation, along with the signature of kinesthetic re-alignment. Indeed, we failed to identify any group differences on these measures. In the rest of this discussion, we evaluate these results with respect to the two theoretical models of implicit sensorimotor adaptation.

Superficially, the fact that implicit adaptation is preserved in deafferented individuals would appear to be in accord with visuo-centric models given that these models do not posit a role for proprioception. However, these models do not provide an account of kinesthetic re-alignment in both normal and deafferented individuals. We can consider different ways in which a visuo-centric model might treat kinesthetic information. In a 'strong' version, one might assume that the adaptation system is immune to multi-sensory integration, with the SPE defined solely by the difference between the target and visual feedback. By this view, perceived hand position is determined only by the location of the visual feedback, remaining fixed throughout the experiment. The hand report results from the deafferented individuals are at odds with this assumption.

Alternatively, a "softer" version is that perceived hand position may be subject to multisensory influences, including a bias introduced by the displaced cursor that is offset over time in a manner similar to that proposed by the kinesthetic re-alignment model. However, by this version of a visuo-centric model, the change in kinesthetic experience would operate in parallel with adaptation, but not drive that learning process. While consistent with the current results, this hypothesis is not parsimonious on empirical and ecological grounds. Empirically, this version of a visuo-centric model does not provide a mechanistic account of the correlation between the extent of kinesthetic bias towards vision and the extent of implicit

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adaptation, a correlation observed in multiple studies (Cressman & Henriques, 2011; Simani et al., 2007; Tsay, Kim, et al., 2021). Ecologically, this view fails to address the ultimate purpose of reaching, to successfully align the desired and felt hand position (e.g., grasp an object).

The kinesthetic re-alignment model can capture two core features of the results, the persistence of adaptation and shift in perceived hand position in the deafferented individuals. Even in the absence of proprioceptive afferents, the introduction of the visual clamp will induce a bias in perceived hand position and, thus, yield a kinesthetic SPE, the signal that drives adaptation. In the original version of the model, adaptation to clamped feedback was proposed to reach asymptote when the bias in perceived hand position towards the clamp is offset by proprioceptive feedback from the adapted hand; for example, proprioceptive signals from a hand that is shifted 20° in the opposite direction of the clamp is sufficient to offset a 5° kinesthetic shift inducted by the clamp. By this view, we had predicted that the extent of adaptation would be heightened in the deafferented group. In the extreme, adaptation should continue unchecked since there is no proprioceptive input to offset the visual signal. If we assume that some residual, noisy proprioceptive input remains intact in deafferented participants, the extent of adaptation should be elevated since a larger shift in actual hand position would be required to nullify the visually induced kinesthetic shift. This prediction was not supported by the data, indicating that the original re-alignment model requires modification.

The kinesthetic re-alignment model did address how non-sensory information influenced perceived hand position. In particular, we mentioned how the target location not only defines the movement goal (i.e., the sensory prediction), but also serves as a prior, one that may be combined with afferent signals to define the perceived hand position. To accommodate the current results, we propose to include a second non-sensory input to kinesthesia, a sensory prediction arising from the actual motor command (Figure 3) (Gandevia et al., 2006; D. M. Wolpert et al., 1995). Whereas the prior remains invariant (i.e., the intended movement goal remains at the target), the motor command changes over time as it recalibrates the mapping between the movement goal and the sensorimotor system. With this added efferent signal, proprioceptive afferents are no longer the sole signal that counterbalances the kinesthetic bias towards vision during implicit adaptation. The efferent-based sensory prediction provides another signal to nullify the kinesthetic SPE.

Our data can be interpreted through the lens of this revised kinesthetic re-alignment model. If we assume that one of these signals, the proprioceptive input, is weakened in deafferented individuals, we would expect a larger asymptote in this group, similar to the prediction derived from the original re-alignment model. However, it is unlikely that the afferent and efferent signals make separable contributions given that they essentially signal the same information — the position of the hand following movement. That is, these two signals may be weighted to form a composite signal of actual hand position. In chronically deafferented individuals, this composite must be dominated by the efferent signal (Bard et al., 1999; Bernier et al., 2006; Fleury et al., 1995; Sarlegna et al., 2006). By the revised kinesthetic re-alignment model, we infer that this re-weighted signal in deafferented participants is equally effective in counteracting a visually-induced kinesthetic error as that available to control participants.

We recognize that this revision of the kinesthetic re-alignment model requires direct empirical interrogation. Tendon vibration (Eschelmuller et al., 2021; Inglis & Frank, 1990) would disrupt proprioception in control participants. Assuming that re-weighting does not occur immediately, we expect that this manipulation would result in a weaker composite signal, and therefore, heightened implicit adaptation.

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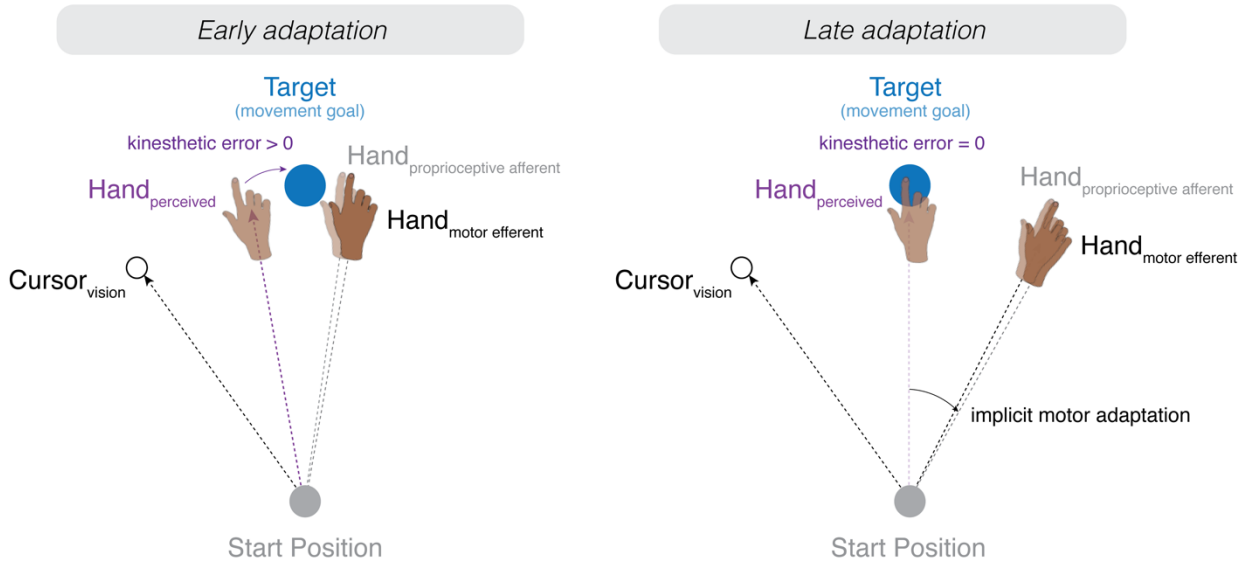

Figure 3: A revised kinesthetic re-alignment model of implicit adaptation. According to the kinesthetic re-alignment model, the goal of implicit adaptation is to minimize a kinesthetic error (error = perceived hand position – movement goal). The perceived hand position is a composite signal that integrates signals from proprioceptive afferents, the efferent motor command, vision (the visual cursor position), and a prior belief that the movement is successful. The extent of implicit adaptation will correspond to the point in which the kinesthetic error is nullified, that is, when the perceived hand position is re-aligned with the movement goal (right panel).

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Methods

Ethics Statement

All participants gave written informed consent in accordance with policies approved by the UC Berkeley's Institutional Review Board. 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 combination, we used an online approach to test six chronic, deafferented participants spread across four countries (Tables 1-2). This sample is larger and more etiologically diverse than recruited in prior studies on this topic. Three participants have a congenital disorder that affects proprioception and tactile perception, and results in severe motor ataxia: CM and SB have an autosomal recessive mutations in the mechanoreceptor PIEZO2 gene (Chesler et al., 2016). CD has an inherited mutation in the mechanoreceptor ASIC3 gene (Lin et al., 2016). The three other participants had acquired deafferentation following an acute neurological episode. IW suffered a sensory neuropathy at age 19 from an autoimmune response to a viral infection. This resulted in severe proprioceptive and tactile impairments below the neck (Cole & Katifi, 1991; Cole & Sedgwick, 1992). WL had a bout of polyradiculitis at age 31 which resulted in severe proprioceptive and tactile impairments below the neck (Miall et al., 2018, 2019). DC has a severe proprioceptive impairment in the right upper limb subsequent to surgical resection at age 38 of a vascular tumor near the right medulla oblongata (Cardinali et al., 2016; Miller et al., 2019).

A total of 60 control participants were recruited, with 10 controls selected to match one of the deafferented participants in terms of age, sex, handedness, and device used in the experiment (Table 2). Control participants were recruited via Prolific, an online crowdsourcing platform connecting researchers to willing participants around the world.

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.

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

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, 5 Trackpad
Control	60	45.1 (14.9)	20M, 40F	45R, 15L	16 Mouse, 44 Trackpad

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: $\chi^2(1, 66) = 0, p = 1$; Handedness: $\chi^2(1, 66) = 0.2, p = 0.66$; Device used: $\chi^2(1, 66) = 0.3, p = 0.59$).

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Apparatus

Participants used their own computer to access a dynamic webpage (HTML, JavaScript, and CSS) hosted on Google Firebase (Tsay, Lee, et al., 2021). The task progression was controlled by JavaScript code running locally in the participant's web browser. The size and position of stimuli were scaled based on the participant's screen size, which was automatically detected. There was no 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).

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 (Tsay, Lee, et al., 2021). Moreover, based on our informal observations, participants remain focused on the screen during the experiment (to see the target and how well they are doing). As such, vision of the hand would be limited.

Procedure

Participants used either a trackpad or mouse to move a computer cursor (see a video describing the task here: https://youtu.be/6eJ78sQsjF8). Participants made a center-out movement from the center of the workspace to a visual target. A white annulus (0.5 cm in diameter) indicated the center position, the cursor was a white dot (0.5 cm in diameter) and a blue circle indicated the target location (0.5 cm in diameter). There were four possible target locations equally spaced around the workspace (45°, 135°, 225°, 315°; 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 (within the perimeters of the trackpad/tabletop), determined by participants' device sensitivity (gain) settings. Although we did not specify how the movements should be performed, the movements were largely restricted to movement about the wrist and fingers given the device and required movement distance.

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 hand 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 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 hand left the start annulus and remained off for the entire reach. During veridical feedback trials, the movement direction of the cursor was veridical with respect to the movement direction of the hand. The veridical cursor was extinguished when the hand crossed the radial target distance of 8 centimeters. Note that veridical feedback trials were only used at the beginning of the experiment to familiarize the participant with the task. During clamped feedback trials (Figure 1A), the cursor moved at a 30° angular offset relative to the position of the target, counterclockwise and irrespective of the actual movement direction of the hand – a manipulation shown to isolate implicit adaptation (Morehead et al., 2017; Tsay et al., 2020). The clamped cursor was extinguished when the hand crossed the radial target distance of 8 centimeters.

Every 10th cycle, participants were asked to report their perceived hand position for four consecutive trials (i.e., one report per target location). There were a total of 40 'kinesthetic report' trials over the course of the experiment. On kinesthetic report trials, a number wheel appeared on the screen following the completion of the center-out movement, 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

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number "1" positioned at the target location. The participant used the keyboard to report the number closest to their perceived hand 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 reaches 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, three demonstration trials were provided before the first perturbation block. On all three trials, the target appeared straight ahead (90° position), and the participant was told to reach to the left (Demo 1), to the right (Demo 2) and backward (Demo 3). On all three of these demonstration trials, the cursor moved in a straight line, 90° offset from the target. In this way, the participant could see that the spatial trajectory of the cursor was unrelated to their own reach direction.

To verify that the participants understood the clamped visual feedback manipulation task, we included an instruction check after the three demonstration trials. 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.

Data analysis

The main dependent variable for measuring adaptation was hand angle, defined as the angle of the hand relative to the target when movement amplitude reached 8 cm from the start position. This measure defines the angular difference between the target location and movement direction. Pilot work using our web-based platform indicated that reaching trajectories are generally fast and straight without evidence of online feedback corrections.

Baseline was defined as the mean hand angle during the initial no-visual feedback block. To evaluate the magnitude of adaptation, the hand angle for each trial was calculated with respect to the participant's idiosyncratic no-feedback baseline bias, calculated separately for each target (cycles 1 – 40). We defined three *a priori* phases of adaptation: Early adaptation, late adaptation, and aftereffect. Early adaptation was operationalized as the mean hand angle over the first 20 cycles of the clamped visual feedback block (cycles 41 – 60). Late adaptation was defined as the mean hand angle over the last 20 cycles of the clamped visual feedback block (cycles 81 – 100). The aftereffect was operationalized as the mean hand angle over the 10 cycles of the no-feedback aftereffect block (cycles 101 – 110).

Outlier responses were defined as trials in which the hand 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 location or attentional lapses (average excluded movement trials: Control group = 1.3 ± 0.2%; Deafferented group = 1.1 ± 0.3%).

The kinesthetic reports provide the dependent variable for measuring perceived hand position. These data were converted into angular values, although we note that the kinesthetic reports involve categorical data (numbers spaced at 6° intervals), whereas in angular form they suggest a continuous variable. The

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kinesthetic report data were baseline corrected on an individual basis to account for idiosyncratic report biases for the four target locations and summarized over the three phases of adaptation. Outlier responses were removed in the exact same manner as the hand angle data (average excluded report trials: Control group = 1.8 ± 1.0%; Deafferented group = 0.4 ± 0.4%).

Reaction time was defined as the time from target presentation to the start of movement, defined as when the radial movement of the hand exceeded 1 cm of movement. Movement time was defined as the time between the start of movement and when the radial extent of the visual cursor (either hidden or provided) reached 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.

Data were statistically analyzed using a linear mixed effect model (R: lmer function) with Phase (early, late and aftereffect) and Group (Deafferented, Control) as fixed (interacting) factors and Participant as a random factor. Post hoc two-tailed t-tests on the betas 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 can not 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). To complement our linear regression analysis, we also fit each individual's data using non-linear regression (Michaelis-Menten curve) (R function: *drm*).

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References

Albert, S. T., Jang, J., Modchalingam, S., 't Hart, M., Henriques, D., Lerner, G., Della-Maggiore, V., Haith, A. M., Krakauer, J. W., & Shadmehr, R. (2022). Competition between parallel sensorimotor learning systems. *ELife*, *11*. https://doi.org/10.7554/eLife.65361

Albert, S. T., Jang, J., Sheahan, H. R., Teunissen, L., Vandevoorde, K., Herzfeld, D. J., & Shadmehr, R. (2021). An implicit memory of errors limits human sensorimotor adaptation. *Nature Human Behaviour*. https://doi.org/10.1038/s41562-020-01036-x

Bard, C., Turrell, Y., Fleury, M., Teasdale, N., Lamarre, Y., & Martin, O. (1999). Deafferentation and pointing with visual double-step perturbations. *Experimental Brain Research*, *125*(4), 410–416.

Bernier, P.-M., Chua, R., Bard, C., & Franks, I. M. (2006). Updating of an internal model without proprioception: a deafferentation study. *Neuroreport*, *17*(13), 1421–1425.

Burge, J., Ernst, M. O., & Banks, M. S. (2008). The statistical determinants of adaptation rate in human reaching. *Journal of Vision*, *8*(4), 20.1-19.

Cardinali, L., Brozzoli, C., Luauté, J., Roy, A. C., & Farnè, A. (2016). Proprioception Is Necessary for Body Schema Plasticity: Evidence from a Deafferented Patient. *Frontiers in Human Neuroscience*, *10*, 272.

Chesler, A. T., Szczot, M., Bharucha-Goebel, D., Čeko, M., Donkervoort, S., Laubacher, C., Hayes, L. H., Alter, K., Zampieri, C., Stanley, C., Innes, A. M., Mah, J. K., Grosmann, C. M., Bradley, N., Nguyen, D., Foley, A. R., Le Pichon, C. E., & Bönnemann, C. G. (2016). The role of PIEZO2 in human mechanosensation. *The New England Journal of Medicine*, *375*(14), 1355–1364.

Cole, J. (1991). *Pride and a Daily Marathon*. Gerald Duckworth.

Cole, J., & Katifi, H. A. (1991). Evoked potentials in a man with a complete large myelinated fibre sensory neuropathy below the neck. *Evoked Potentials*, *80*(2), 103–107.

Cole, J., & Sedgwick, E. M. (1992). The perceptions of force and of movement in a man without large myelinated sensory afferents below the neck. *The Journal of Physiology*, *449*(1), 503–515.

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Cressman, E. K., & Henriques, D. Y. P. (2011). Motor adaptation and proprioceptive recalibration. *Progress in Brain Research*, *191*, 91–99.

Cressman, E. K., Salomonczyk, D., & Henriques, D. Y. P. (2010). Visuomotor adaptation and proprioceptive recalibration in older adults. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *205*(4), 533–544.

Donchin, O., Francis, J. T., & Shadmehr, R. (2003). Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *The Journal of Neuroscience*, *23*(27), 9032–9045.

Edin, B. B., & Johansson, N. (1995). Skin strain patterns provide kinaesthetic information to the human central nervous system. *The Journal of Physiology*, *487*(1), 243–251.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433.

Eschelmuller, G., Chua, R., Carpenter, M. G., & Inglis, J. T. (2021). The acute effects of periodic and noisy tendon vibration on wrist muscle stretch responses. *Neuroscience Letters*, *764*, 136279.

Fassold, M. E., Locke, S. M., & Landy, M. S. (2022). Feeling lucky? Prospective and retrospective cues for sensorimotor confidence. In *bioRxiv*. https://doi.org/10.1101/2022.11.15.516696

Ferrea, E., Morel, P., Franke, J., & Gail, A. (2021). Statistical determinants of visuomotor adaptation in a virtual reality three-dimensional environment. In *Cold Spring Harbor Laboratory* (p. 2021.02.16.431440). https://doi.org/10.1101/2021.02.16.431440

Fleury, M., Bard, C., Teasdale, N., Paillard, J., Cole, J., Lajoie, Y., & Lamarre, Y. (1995). Weight judgment. *Brain: A Journal of Neurology*, *118*(5), 1149–1156.

Franklin, D. W., So, U., Burdet, E., & Kawato, M. (2007). Visual feedback is not necessary for the learning of novel dynamics. *PloS One*, *2*(12), e1336.

Gandevia, S. C., Smith, J. L., Crawford, M., Proske, U., & Taylor, J. L. (2006). Motor commands contribute to human position sense. *The Journal of Physiology*, *571*(Pt 3), 703–710.

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Herzfeld, D. J., Vaswani, P. A., Marko, M. K., & Shadmehr, R. (2014). A memory of errors in sensorimotor learning. *Science*, *345*(6202), 1349–1353.

Inglis, J. T., & Frank, J. S. (1990). The effect of agonist/antagonist muscle vibration on human position sense. *Experimental Brain Research*, *81*(3), 573–580.

Ingram, H. A., van Donkelaar, P., Cole, J., Vercher, J. L., Gauthier, G. M., & Miall, R. C. (2000). The role of proprioception and attention in a visuomotor adaptation task. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *132*(1), 114–126.

Kim, H. E., Morehead, R., Parvin, D. E., Moazzezi, R., & Ivry, R. B. (2018). Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Communications Biology*, *1*, 19.

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, *427*(6971), 244–247.

Lackner, J. R., & Dizio, P. (1994). Rapid adaptation to Coriolis force perturbations of arm trajectory. *Journal of Neurophysiology*, *72*(1), 299–313.

Lefumat, H. Z., Miall, R. C., Cole, J. D., Bringoux, L., Bourdin, C., Vercher, J.-L., & Sarlegna, F. R. (2016). Generalization of force-field adaptation in proprioceptively-deafferented subjects. *Neuroscience Letters*, *616*, 160–165.

Lin, S.-H., Cheng, Y.-R., Banks, R. W., Min, M.-Y., Bewick, G. S., & Chen, C.-C. (2016). Evidence for the involvement of ASIC3 in sensory mechanotransduction in proprioceptors. *Nature Communications*, *7*, 11460.

Miall, R. C., Kitchen, N. M., Nam, S.-H., Lefumat, H., Renault, A. G., Ørstavik, K., Cole, J. D., & Sarlegna, F. R. (2018). Proprioceptive loss and the perception, control and learning of arm movements in humans: evidence from sensory neuronopathy. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *236*(8), 2137–2155.

bioRxiv preprint doi: https://doi.org/10.1101/2023.01.19.524726; this version posted January 20, 2023. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC 4.0 International license.

Miall, R. C., Rosenthal, O., Ørstavik, K., Cole, J. D., & Sarlegna, F. R. (2019). Loss of haptic feedback impairs control of hand posture: a study in chronically deafferented individuals when grasping and lifting objects. *Experimental Brain Research*, *237*(9), 2167–2184.

Michaelis, L., & Menten, M. (1913). Die kinetik der invertinwirkung. *Biochemistry Zeitung*, *49*, 333–369.

Miller, L. E., Fabio, C., Ravenda, V., Bahmad, S., Koun, E., Salemme, R., Luauté, J., Bolognini, N., Hayward, V., & Farnè, A. (2019). Somatosensory cortex efficiently processes touch located beyond the body. *Current Biology: CB*, *29*(24), 4276-4283.e5.

Morehead, R., & Smith, M. (2017). *The magnitude of implicit sensorimotor adaptation is limited by continuous forgetting*. Advances in Motor Learning & Motor Control. https://groups.seas.harvard.edu/motorlab/Reprints/MLMC2017_abstract_Morehead.pdf

Morehead, R., Taylor, J. A., Parvin, D. E., & Ivry, R. B. (2017). Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience*, *29*(6), 1061–1074.

Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, *92*(4), 1651–1697.

Rand, M., & Heuer, H. (2019). Visual and proprioceptive recalibrations after exposureto a visuomotor rotation. *The European Journal of Neuroscience*, *50*, 3296–3310.

Rossi, C., Bastian, A. J., & Therrien, A. S. (2021). Mechanisms of proprioceptive realignment in human motor learning. *Current Opinion in Physiology*, *20*, 186–197.

Rothwell, J. C., Traub, M. M., Day, B. L., Obeso, J. A., Thomas, P. K., & Marsden, C. D. (1982). Manual motor performance in deafferented man. *Brain: A Journal of Neurology*, *105*(3), 515–542.

Ruttle, J. E., Hart, B. M. ’t, & Henriques, D. Y. P. (2021). Implicit motor learning within three trials. *Scientific Reports*, *11*(1), 1627.

Sarlegna, F. R., Gauthier, G. M., Bourdin, C., Vercher, J.-L., & Blouin, J. (2006). Internally driven control of reaching movements: a study on a proprioceptively deafferented subject. *Brain Research Bulletin*, *69*(4), 404–415.

bioRxiv preprint doi: https://doi.org/10.1101/2023.01.19.524726; this version posted January 20, 2023. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC 4.0 International license.

Sarlegna, F. R., Malfait, N., Bringoux, L., Bourdin, C., & Vercher, J.-L. (2010). Force-field adaptation without proprioception: can vision be used to model limb dynamics? *Neuropsychologia*, *48*(1), 60–67.

Sarlegna, F. R., & Sainburg, R. L. (2009). The roles of vision and proprioception in the planning of reaching movements. *Advances in Experimental Medicine and Biology*, *629*, 317–335.

Shadmehr, R., Smith, M. A., & Krakauer, J. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience*, *33*, 89–108.

Simani, M. C., McGuire, L. M. M., & Sabes, P. N. (2007). Visual-shift adaptation is composed of separable sensory and task-dependent effects. *Journal of Neurophysiology*, *98*(5), 2827–2841.

Smeets, J. B. J., van den Dobbelsteen, J. J., de Grave, D. D. J., van Beers, R. J., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(49), 18781–18786.

Sober, S. J., & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, *8*(4), 490–497.

Sterman, A. B., Schaumburg, H. H., & Asbury, A. K. (1980). The acute sensory neuronopathy syndrome: a distinct clinical entity. *Annals of Neurology*, *7*(4), 354–358.

Synofzik, M., Thier, P., Leube, D. T., Schlotterbeck, P., & Lindner, A. (2010). Misattributions of agency in schizophrenia are based on imprecise predictions about the sensory consequences of one's actions. *Brain: A Journal of Neurology*, *133*(Pt 1), 262–271.

Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, *407*(6805), 742–747.

Tsay, J. S., Kim, H. E., Parvin, D. E., Stover, A. R., & Ivry, R. B. (2021). Individual differences in proprioception predict the extent of implicit sensorimotor adaptation. *Journal of Neurophysiology*. https://doi.org/10.1152/jn.00585.2020

Tsay, J. S., Kim, H., Haith, A. M., & Ivry, R. B. (2022). Understanding implicit sensorimotor adaptation as a process of proprioceptive re-alignment. *ELife*, *11*. https://doi.org/10.7554/eLife.76639

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Tsay, J. S., Lee, A., Ivry, R. B., & Avraham, G. (2021). Moving outside the lab: The viability of conducting sensorimotor learning studies online. *Neurons, Behavior, Data Analysis, and Theory*. http://arxiv.org/abs/2107.13408

Tsay, J. S., Parvin, D. E., & Ivry, R. B. (2020). Continuous reports of sensed hand position during sensorimotor adaptation. *Journal of Neurophysiology*, *124*(4), 1122–1130.

van der Kooij, K., Brenner, E., van Beers, R. J., Schot, W. D., & Smeets, J. B. J. (2013). Alignment to natural and imposed mismatches between the senses. *Journal of Neurophysiology*, *109*(7), 1890–1899.

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, *269*(5232), 1880–1882.

Wolpert, Daniel M., Diedrichsen, J., & Randall Flanagan, J. (2011). Principles of sensorimotor learning. In *Nature Reviews Neuroscience* (Vol. 12, Issue 12, pp. 739–751). https://doi.org/10.1038/nrn3112

Yousif, N., Cole, J., Rothwell, J., & Diedrichsen, J. (2015). Proprioception in motor learning: lessons from a deafferented subject. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *233*(8), 2449–2459.