



Improved proprioception does not benefit visuomotor adaptation

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Abstract

Visuomotor adaptation arises when reaching in an altered visual environment, where one's seen hand position does not match their felt (i.e., proprioceptive) hand position in space. Here, we asked if proprioceptive training benefits visuomotor adaptation, and if these benefits arise due to implicit (unconscious) or explicit (conscious strategy) processes. Seventy-two participants were divided equally into 3 groups: proprioceptive training with feedback (PTWF), proprioceptive training no feedback (PTNF), and Control (CTRL). The PTWF and PTNF groups completed passive proprioceptive training, where a participant's hand was moved to an unknown reference location and they judged the felt position of their unseen hand relative to their body midline on every trial. The PTWF group received verbal feedback with respect to their response accuracy on the middle 60% of trials, whereas the PTNF did not receive any feedback during training. The CTRL group did not complete proprioceptive training and instead sat quietly during this time. Following proprioceptive training or time delay, all three groups reached when seeing a cursor that was rotated 30° clockwise relative to their hand motion. The experiment ended with participants completing a series of no-cursor reaches to assess implicit and explicit adaptation. Results indicated that the PTWF group improved the accuracy of their sense of felt hand position following proprioceptive training. However, this improved proprioceptive acuity (i.e., the accuracy of their sense of felt hand) did not benefit visuomotor adaptation, as all three groups showed similar visuomotor adaptation across rotated reach training trials. Visuomotor adaptation arose implicitly, with minimal explicit contribution for all three groups. Together, these results suggest that passive proprioceptive training does not benefit, nor hinder, the extent of implicit visuomotor adaptation established immediately following reach training with a 30° cursor rotation.

Keywords Proprioceptive training · Visuomotor adaptation · Implicit · Explicit

Introduction

Proprioceptive training has been shown to benefit motor learning for both patient populations (Carey et al. 2005, 2011; Blennerhassett et al. 2006, 2007) and healthy participants (Wong et al. 2012; Darainy et al. 2013; McGregor et al. 2018). More specifically, for healthy participants, prior proprioceptive training has been shown to benefit motor adaptation when participants reach in a velocity-dependent forcefield (Darainy et al. 2013; McGregor et al. 2018). Within forcefield adaptation paradigms, participants

typically reach to a target in a virtual environment while experiencing a clockwise (CW) or counter-clockwise (CCW) force that pushes their hand in the horizontal direction, perpendicular to a movement vector connecting the reach starting position and target (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Mattar and Gribble 2005). Initial reaching errors when reaching in a velocity-dependent forcefield are common, such that trajectories are curved and the hand may not land on the target as expected (Scheidt et al. 2001; Donchin et al. 2003; Ostry et al. 2010). Over trials, participants adapt their reaches to this new environment by pushing their hand in the opposite direction of the forcefield. In recent work, Darainy and colleagues (2013) and McGregor and colleagues (2018) have shown that reach adaptation occurs earlier if participants have completed proprioceptive training.

Darainy and colleagues' (2013) proprioceptive training included having participants judge the felt position of

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their unseen hand relative to their body midline within a hand positioning task. For these trials, their hand was passively moved to an unseen reference location within 8° of their body midline and participants made a judgment about whether the position of their hand was located to the left or to the right of their body midline. One group received verbal feedback indicating if their response was correct or incorrect, whereas another group did not receive any feedback during proprioceptive training, nor did they judge their felt hand position. Proprioceptive acuity (i.e., accuracy in hand judgments) was shown to improve across proprioceptive training trials, but only for the group that provided judgments of felt hand position and received verbal feedback during training. This enhanced proprioceptive acuity was then shown to benefit reach adaptation to the velocity-dependent forcefield compared to the group that did not receive feedback and a Control group of participants that did not complete the proprioceptive training trials. Specifically, these participants' reaches were initially less curved when first introduced to the forcefield compared to participants that had not undergone proprioceptive training with feedback.

Traditionally, motor adaptation when reaching in a velocity-dependent forcefield is presumed to reflect implicit (i.e., unconscious) changes in reaches that arise in response to experiencing a sensory prediction error signal. Specifically, participants experience a discrepancy between the predicted sensory outcome of their movement (e.g., seen position of the hand landing on the target) and the actual sensory feedback experienced (e.g., seen position of the hand heads away from the target; Tseng et al. 2007; Sarlegna and Bernier 2010). To resolve this sensory prediction error, the internal model for reaching is updated to reduce future reaching errors (Wolpert et al. 1995; Shadmehr et al. 2010). More recently, changes in proprioceptive processing have also been implicated in forcefield adaptation (Ostry et al. 2010), with Vahdat et al. (2014) demonstrating that proprioceptive training results in changes to frontal motor areas of the brain, potentially contributing directly to motor adaptation.

Having determined that proprioceptive training benefits forcefield adaptation, we asked if similar benefits arise within a visuomotor adaptation paradigm. Visuomotor adaptation is typically studied by having participants reach in a virtual environment where a cursor on the screen misrepresents the location of their felt hand position in space (Ghahramani et al. 1996; Krakauer et al. 1999; Krakauer et al. 2000; Cressman and Henriques 2009). Similar to forcefield adaptation paradigms, visuomotor adaptation studies introduce a sensory prediction error signal, such that the expected sensory consequences of the movement (i.e., hand/cursor landing on the target) do not match the actual sensory feedback experienced (i.e., hand/cursor does not land on the target as expected). If proprioceptive training primes cortical somatosensory and motor areas, as suggested by McGregor

et al. (2018), see also Vahdat et al. (2014), one would expect visuomotor adaptation to also benefit from enhanced proprioceptive acuity.

Alternatively, proprioceptive training may hinder visuomotor adaptation. Unique to visuomotor adaptation paradigms, it has been suggested that changes in felt limb position arise in response to participants experiencing a cross-sensory error signal when reaching due to the conflict between visual (seen cursor) and proprioceptive (felt) judgments of hand position (Cressman and Henriques 2009; Salomonczyk et al. 2013; Maksimovic et al. 2020). Specifically, proprioception is recalibrated such that one shifts the felt position of their hand in the direction of the distorted visual feedback to once again form a coherent judgment of hand position (Cressman and Henriques 2009, 2010; Salomonczyk et al. 2011, 2012, 2013; Mostafa et al. 2014). This proprioceptive recalibration has been implicated in visuomotor adaptation (Cressman and Henriques 2010). Improvements in proprioceptive acuity may, thus, hinder visuomotor adaptation, as a more accurate estimate of felt hand position may be difficult to recalibrate.

It is currently unclear how enhancing proprioceptive acuity would influence visuomotor adaptation, including the engagement of implicit and explicit processes, where explicit processes refer to the engagement of conscious strategies. Recent methods, including the Process Dissociation Procedure as described below (Werner et al. 2015), have been developed to investigate the contribution of implicit and explicit processes to visuomotor adaptation. To date, sensory changes have been assumed to arise implicitly (Modchalingam et al. 2019) and, hence, contribute to implicit visuomotor adaptation. Addressing current questions regarding the role of enhanced proprioceptive acuity on implicit and explicit visuomotor adaptation would provide insight into the general role of the somatosensory system in motor learning.

To determine the impact of proprioceptive training on visuomotor adaptation, three groups of participants were included in our study, where two of the three groups completed passive proprioceptive training prior to visuomotor adaptation as done by McGregor and colleagues (2018) (see also Darainy 2013). The first group of participants received verbal feedback regarding their judgments of felt hand position after their hand was passively moved into position, and another group completed the proprioceptive judgments, but did not receive any feedback regarding their responses during training as done by McGregor et al. (2018). Requiring our second group to judge the position of their hand in the absence of feedback ensured that all participants receiving proprioceptive training were required to pay attention to the position of their hand, enabling us to isolate the role of training (i.e., feedback) on changes in proprioceptive acuity. As well, based on judgments from all participants, we were

able to determine for which groups proprioceptive acuity improved with training. A third group did not complete proprioceptive training and served as a Control group. Visuomotor adaptation was then assessed in all three groups by having them reach with rotated cursor feedback (30° CW). Finally, to establish the contributions of implicit and explicit processes to visuomotor adaptation, we had participants complete a series of reaches to the targets in the absence of cursor (i.e., visual) feedback. During these trials, participants were instructed to refrain from using (only implicit adaptation assessed), or use (implicit + explicit adaptation assessed) any learned strategy while reaching in the absence of cursor feedback, as done by Werner and colleagues using the Process Dissociation Procedure (2015; see also Neville and Cressman 2018).

We hypothesized that proprioceptive training would benefit visuomotor adaptation, as improving proprioceptive acuity has been suggested to prime cortical somatosensory and motor areas (McGregor et al. 2018). Thus, we expected that the group that received verbal feedback during proprioceptive training would adapt their reaches quicker when first introduced to the visuomotor distortion compared to the group that did not receive feedback during training and the Control group. Alternatively, if no benefits were found, our results would suggest that improving proprioceptive acuity does not benefit, and may even hinder visuomotor adaptation, as an improved sense of proprioception may be harder to recalibrate when first learning to reach with the visuomotor distortion. We also expected motor adaptation to arise implicitly rather than explicitly, as adaptation has been shown to arise implicitly for small visuomotor distortions (i.e., cursor rotations equal to, or less than, 30°), when a small target error signal is experienced (Neville and Cressman 2018; Modchalingam et al. 2019; Vachon et al. 2020).

Methods

Participants

Initial sample size ($n=45$) was determined by performing a power analysis using G*Power (Version 3.1.9.3; Faul et al. 2007), with a desired power of 0.80, a probability of Type 1 error of 0.05, and an expected effect size of 0.14 with respect to the benefit of proprioceptive training (Darainy et al. 2013; McGregor et al. 2018). Given the interest in our study in the University community, we were fortunate to recruit a total of 72 participants aged 19–40 years old ($M=23$ years, $SD=3.8$), surpassing our initial sample size goal. The majority of participants ($n=64$) were deemed to be right-handed based on their responses on the modified version of the Edinburgh Handedness Inventory, while the remaining 8 participants were classified as ambidextrous ($M=80.1$,

$SD=24.5$, range = 0–100; Oldfield 1971). All participants reported having no history of neurological, motor, or sensory impairment, and had normal or corrected-to-normal vision. As well, all participants were naïve to the purpose of the study and had never participated in a visuomotor adaptation study involving reaching with distorted visual feedback in a virtual environment. Participant recruitment and data collection commenced after the Faculty of Health Sciences at the University of Ottawa approved a Safe Research plan and ethical approval was attained from the University of Ottawa's Health Sciences and Science Research Ethics Board. Prior to starting the experiment, all participants provided written informed consent, including the University of Ottawa's Consent Information Addendum—COVID-19 Risks.

Apparatus

Testing took place in a secluded dark room. Participants grasped the handle of the KINARM End-Point Lab (KINARM Technologies, Kingston, ON), using their right hand. As shown in Fig. 1A, visual targets were projected from a downward facing monitor (LG 47LD452B-UA EzSign-47" LCD TV; refresh rate: 60 Hz, 2.6A; Seoul, South Korea) located 20.5 cm above a reflective surface that was located 20.5 cm above the robot handle. Thus, visual stimuli appeared to lie in the same horizontal plane as the right hand holding the robot handle. Participants were seated in a height-adjustable chair located in front of the experimental apparatus (Fig. 1A). The chair was positioned so that the participant's forehead rested comfortably against the testing apparatus and they could reach to all the targets within the workspace. As well, their body midline was aligned with the starting home position and a central target position prior to beginning the experiment (Fig. 1B). The position of the chair was locked in place and maintained throughout the experimental session. Participants' view of their limbs was occluded by the reflective surface and a black cloth that was draped around their neck and attached to the apparatus. Once participants were seated comfortably, the room lights were turned off and testing began.

Experiment overview

General overview

Testing took place during a single session that lasted approximately 1.5 h. Participants were randomly divided into 3 groups ($n=24$ /group): proprioceptive training with feedback (PTWF), proprioceptive training no feedback (PTNF) and Control (CTRL). Depending on group, participants completed the blocks of reaches and proprioceptive training as outlined below (see Fig. 2).

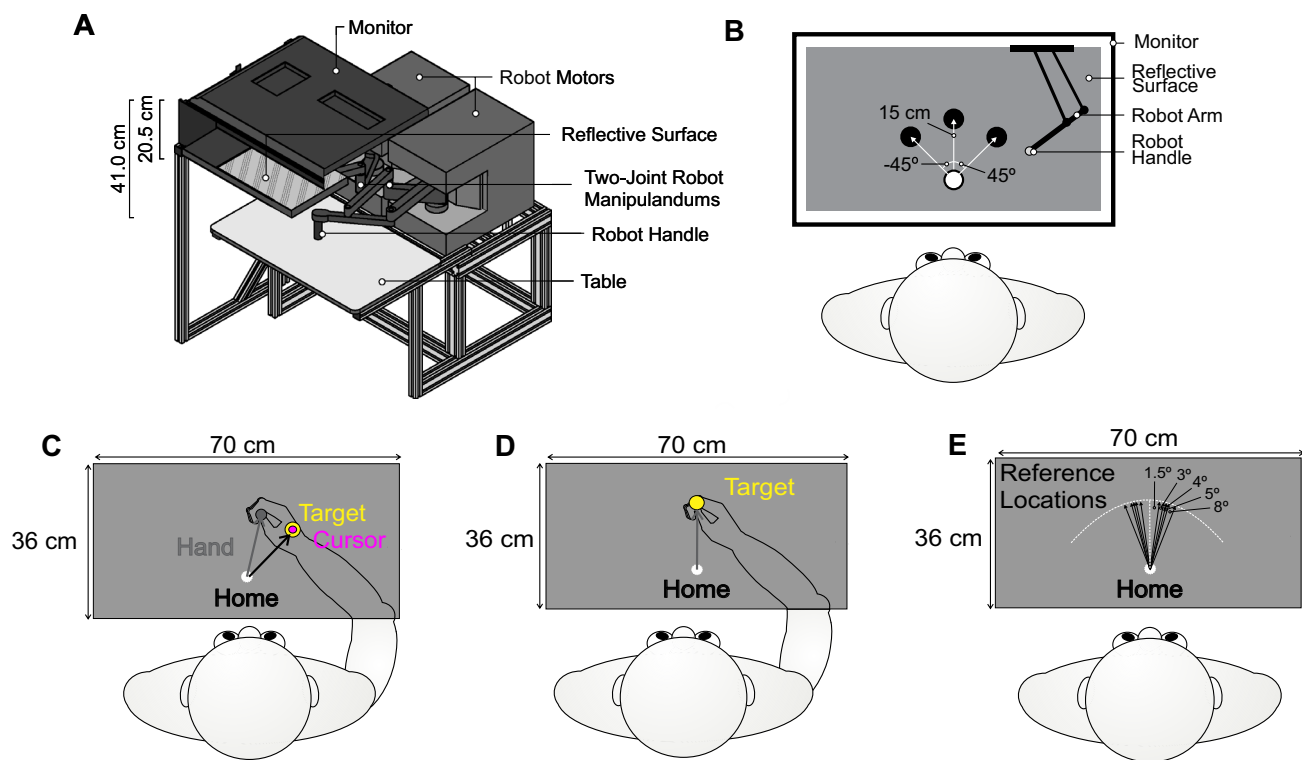


Fig. 1 Experimental apparatus and types of trials. **A** Side view of the experimental apparatus. Participants were instructed to grasp the robot handle with their right hand. **B** Top-down view of the 3 targets that participants reached to during all reaching trials. **C** Rotated Reach Training trials when the cursor was rotated 30° clockwise relative to hand motion. **D** No-Cursor Reaches, when no visual cursor was displayed. **E** The 10 reference locations used in the Proprioceptive Training trials

A Proprioceptive training with feedback (PTWF) & Proprioceptive training no feedback (PTNF)

Aligned Reach Training (Practice)	Aligned Reach Training (Baseline)	No-Cursor Reaches #1	Proprioceptive Training	Aligned Reach Training	No-Cursor Reaches #2	Rotated Reach Training	No-Cursor Reaches #3
9 trials	51 trials	12 trials (2 Blocks)	370 trials (5 Blocks)	15 trials	12 trials (2 Blocks)	99 trials	12 trials (2 Blocks)
1	2	3	4	5	6	7	8

B Control (CTRL)

Aligned Reach Training (Practice)	Aligned Reach Training (Baseline)	No-Cursor Reaches #1	Time Delay	Aligned Reach Training	No-Cursor Reaches #2	Rotated Reach Training	No-Cursor Reaches #3
9 trials	51 trials	12 trials (2 Blocks)		15 trials	12 trials (2 Blocks)	99 trials	12 trials (2 Blocks)
1	2	3	4	5	6	7	8

Fig. 2 Breakdown of testing blocks. **A** Blocks of trials that were completed by the Proprioceptive training with feedback (PTWF) and the Proprioceptive training no feedback (PTNF) groups. **B** Blocks of trials that were completed by the Control (CTRL) group. The Proprioceptive Training consisted of 5 blocks of 74 trials with 2 min breaks after each block. The Time Delay consisted of a 30-min break. No-Cursor reaches #1 and #2 consisted of 2 blocks of 6 trials with exclusion instructions. No-Cursor reaches #3 consisted of 1 block of 6 trials with exclusion instructions, followed by 1 block of 6 trials with inclusion instructions

All reaches began with the participant’s hand at the home position, located approximately 20 cm in front of the participant’s chest (white circle, 2 cm in diameter) and in line with their body midline (Fig. 1B). All three groups first reached while seeing a cursor that was aligned with their hand (i.e., aligned reach training) to establish movement errors in a

typical (i.e., baseline) visual environment (Fig. 1B). All groups then completed a block of no-cursor reaches to determine how they reached to a target when no visual feedback was provided (Fig. 1D). Following this, the PTWF and PTNF groups completed a series of proprioceptive training trials in which their hand was passively moved to a reference location and participants indicated if their hand was located to the left or to the right of their body midline (Fig. 1E). The CTRL group did not complete proprioceptive training and instead stayed seated in the testing room for 30 min (i.e., time delay). Following proprioceptive training or time delay, all participants completed a second block of aligned reaches followed by a second block of no-cursor reaches. These trials were then followed by a block of reaches with a visuomotor distortion (i.e., rotated reach training; Fig. 1C), followed by a third block of no-cursor reaches to assess the contributions of implicit and/or explicit processes to visuomotor adaptation. The number of trials per each block was chosen in accordance with previous research examining the influence of proprioceptive training on motor adaptation (see Darainy et al. 2013; McGregor et al. 2018) or assessing implicit and explicit contributions to visuomotor adaptation (see Neville and Cressman 2018; Heirani Moghaddam et al. 2021).

Reach training trials

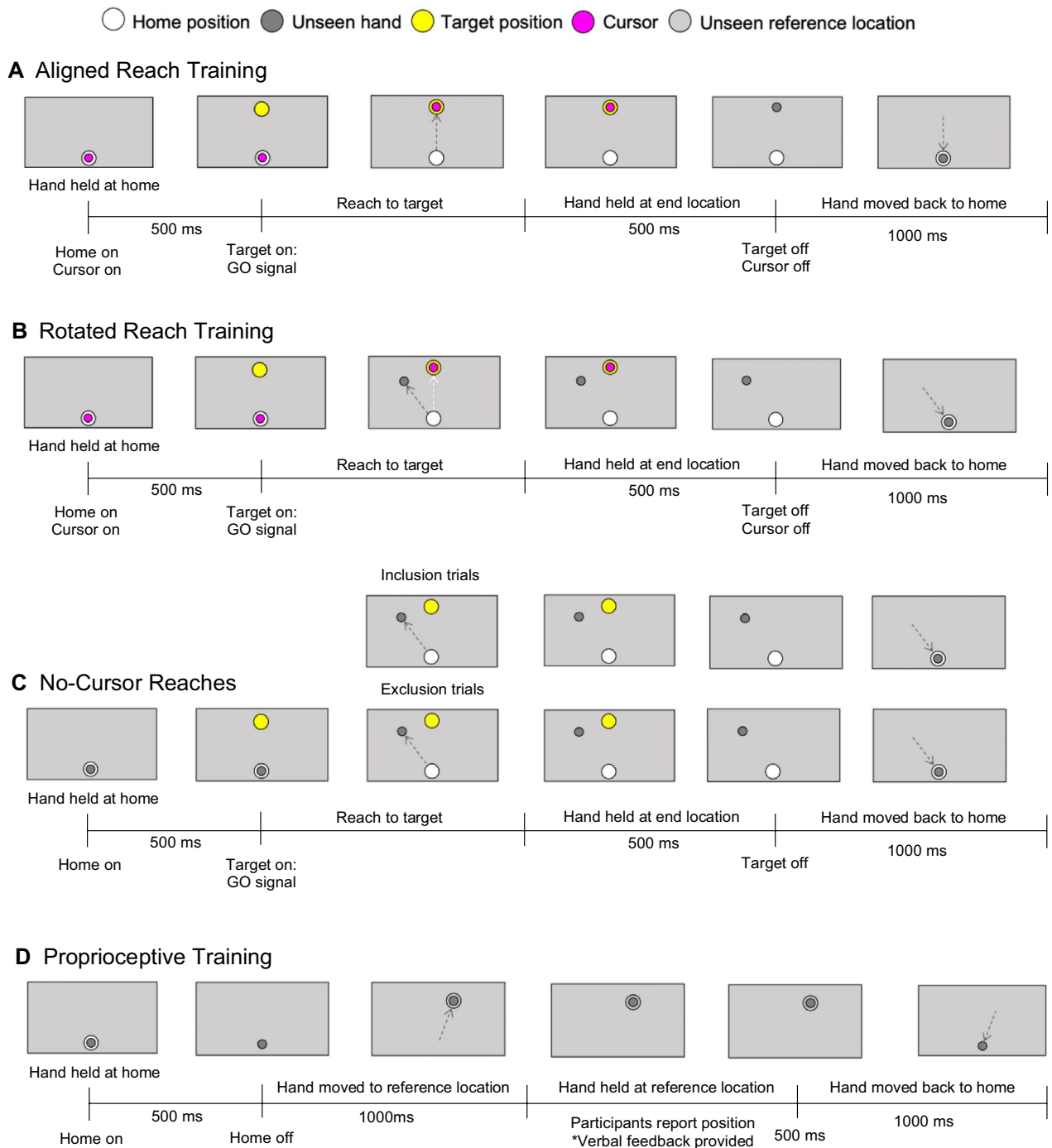
During aligned reach training (Fig. 2A, B, Box 1, 2, 5), all three groups began by holding the robot handle at the home position. Following 500 ms, one of three targets appeared (yellow circle, 2 cm in diameter), located 15 cm away from the home position. The targets were located straight ahead of the home position (central target; 0°) and 45° to the left and right of the central target. Once a target appeared, participants were instructed to reach to it as quickly as possible with the goal of having the cursor land on the target. Real-time visual feedback of the hand position was provided via a cursor on the screen (magenta circle, 1 cm in diameter), both while the hand was held in the home position prior to the start of the reach, and throughout the duration of the movement. Once participants landed on the target (i.e., the center of the cursor and the center of the target were within 0.5 cm), the hand was held at this position for another 500 ms. The cursor and the target then disappeared, and the robot passively moved the hand back to the home position following a direct, linear path in a movement time of 1000 ms. If participants attempted to move outside of the linear path, a resistance force (proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous dampening of 5 N/mm) perpendicular to the grooved path was produced. The position of the KINARM robot was recorded at a sampling rate of 1000 Hz, with a spatial accuracy of 0.1 mm. See Fig. 3A for a timeline of events for aligned reach training.

Participants began by completing 9 practice aligned reach training trials (3 to each target; Fig. 2A & B, Box 1). The practice trials were completed to allow participants to familiarize themselves with the reaching task and were not analyzed. Following the practice trials, participants completed 51 aligned reaches (i.e., 17 to each target; Fig. 2A, B, Box 2) to establish baseline performance. An additional 15 aligned reaches (5 to each target; Fig. 2A, B, Box 5) were completed following proprioceptive training (PTWF and PTNF groups) or the time delay (CTRL group), enabling errors experienced when reaching with the visuomotor distortion described below to be normalized.

The rotated reach training trials (Fig. 2A, B, Box 7) followed the same timeline of events as the aligned reach training trials explained above, in that participants were instructed to reach to the target quickly with the goal of having the cursor land on the target. However, on these trials, the cursor representing the position of the hand was rotated 30° CW relative to the participant's hand trajectory (Fig. 1C). Participants were not made aware of this rotation, nor were they given instruction on how to counteract it. See Fig. 3B for a timeline of events for rotated reach training trials. All 3 groups performed 99 reaches (33 to each target) with the rotated cursor following proprioceptive training or time delay.

No-cursor reaches to assess implicit and explicit adaptation

Two blocks of 6 no-cursor reaches (2 reaches to each target within each block) were performed 3 times: before (i.e., Time 1; Fig. 2A, B, Box 3) and after (i.e., Time 2; Fig. 2A, B, Box 6) proprioceptive training or time delay, and again after rotated reach training (i.e., Time 3; Fig. 2A, B, Box 8). For these trials, participants reached when no visual cursor was displayed (Fig. 1D). These reaches followed the same timeline of events as described above in the reach training trials (see Fig. 3C); however, the end of each movement was determined online as the time at which velocity first decreased below 0.01 m/s. The no-cursor reaches at Time 1 and Time 2 included two blocks of 6 exclusion trials, where participants were instructed to: "Reach so that your hand goes straight to the target". Following the rotated reach training trials (Time 3), participants completed 6 *exclusion* trials. These were then followed by 6 *inclusion* trials, in which participants were asked to: "Reach using anything you have learned during training to get the cursor to the target. In other words, reach so that the cursor would have gone straight to the target, as in the reaching trials you just completed when the cursor was available".



*Feedback re response accuracy was only provided to the Proprioceptive training with feedback (PTWF) group and only during Blocks 2–4 of training.

Fig. 3 Timeline of events for each trial type. **A** Aligned Reach Training trials. **B** Rotated Reach Training trials. **C** No-Cursor Reaches (i.e., exclusion and inclusion trials). **D** Proprioceptive Training trials

Proprioceptive training

The PTWF and PTNF groups completed proprioceptive training (Fig. 2A, Box 4). This training consisted of a hand

positioning task and was conducted in the absence of visual feedback (Fig. 1E). Participants completed 5 blocks of 74 trials, for a total of 370 trials (as done by McGregor et al. 2018). A 2-min break was given at the end of each block,

at which time participants remained seated at the testing apparatus with their hand hidden from view.

Proprioceptive training trials began with a participant's hand held at the home position for 500 ms. After 500 ms, the home position disappeared and the robot passively moved the hand 15 cm outward to one of ten reference locations (RL) located along a circular arc (Fig. 1E). These RL were located at 1.5°, 3°, 4°, 5° and 8° to the left and to the right of center (i.e., 0°, corresponding to body midline; as used by Darainy et al. 2013). The breakdown of trials to each RL in each block was: 10 trials to the 1.5° RL, 10 trials to the 3° RL, 7 trials to the 4° RL, 7 trials to the 5° RL and 3 trials to the 8° RL in the leftwards and rightwards direction relative to center. The RL were presented in a randomized order.

For each trial, the robot moved the participant's hand outwards with a bell-shaped velocity profile with an average speed of 15 cm/s, such that all movements took 1000 ms to complete. Once the hand reached the RL, participants were asked to verbally indicate if the position of their hand was located to the left or to the right of their body midline (i.e., the center of their body). There was no time limit to respond and their response was recorded by the experimenter. No feedback about response accuracy was provided to either group in the first and last block of proprioceptive training trials (i.e., Blocks 1 and 5). However, in the middle blocks of trials (i.e., Blocks 2, 3, and 4), feedback regarding response accuracy was provided to the PTWF group only. Specifically, they were told if their response was “correct” or “incorrect”. The PTNF group did not receive feedback regarding their responses. After responses were recorded for both groups, the hand was held at the RL for an additional 500 ms before being moved directly back to the home position in a time of 1000 ms to start the next trial. See Fig. 3D for a timeline of events for the proprioceptive training trials.

Data analysis

Proprioceptive training

We first looked to establish participants' proprioceptive acuity (i.e., their ability to locate the position of their hand in space) over the course of the proprioceptive training trials by determining a participant's absolute bias (i.e., response accuracy; perceived boundary between left and right of body midline; 50th percentile) and uncertainty range (i.e., response consistency; interquartile range (IQR); distance between the 25th and 75th percentiles). Proprioceptive acuity was determined for each participant in the PTWF and PTNF groups for each of the five blocks of proprioceptive training trials by fitting a binary logistic function to each participant's responses across all reference locations (see Fig. 4). Absolute bias and uncertainty ranges were compared between the PTWF and PTNF groups over the 5 blocks of

proprioceptive training trials using a 2 Group (PTWF and PTNF) \times 5 Block (Blocks 1–5) mixed analysis of variance (ANOVA) with repeated measures (RM) on the second factor.

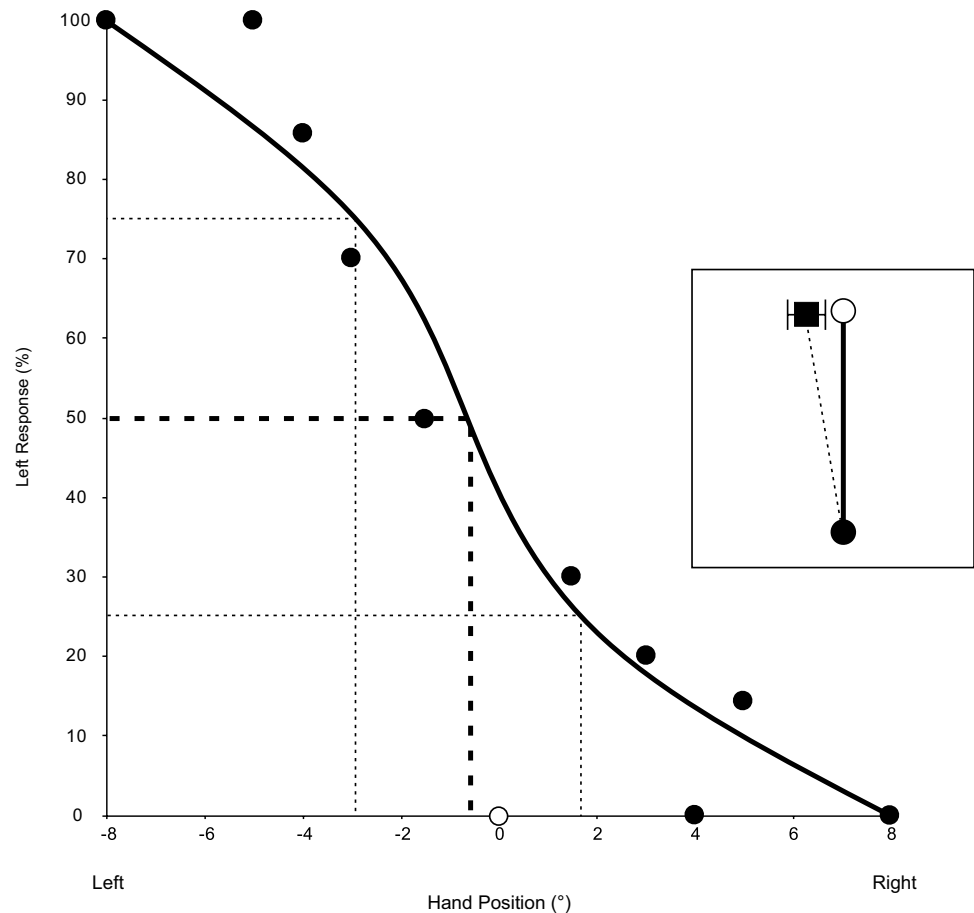
Reaching trials

All reaching trials (i.e., aligned reach training trials, rotated reach training trials, and no-cursor reaches) were visually inspected using custom written programs for MATLAB. The start (i.e., movement onset) and end (i.e., movement termination) points of each movement were selected using a velocity-based criterion such that movement onset and movement termination were defined as when velocity first increased above, and decreased below, 0.01 m/s and remained above or below for 50 ms, respectively. For each trial, we determined the angular error of the hand at peak velocity (i.e., PVAE), where PVAE is equal to the angular difference between a vector from the home position to the desired target and a vector from the home position to the hand's actual position at peak velocity. If participants reached so that the cursor went directly to the target, PVAE would be minimal (i.e., 0°) in the aligned reach training trials and approximately 30° to the left of the target in the rotated reach training trials to account for the visuomotor distortion. Trials were removed from analysis if PVAE was greater than 50° or less than 3 standard deviations (SD) below a participants' average error on the second block of 6 no-cursor exclusion trials following aligned reach training (Fig. 2A, B, Box 3). A maximum cut-off value was chosen in comparison to using the more typical mean + 3SD given the variation in participants' reaching errors when reaching with rotated cursor feedback over time (e.g., PVAE could vary by as much as 30° over the course of rotated reach training trials). Based on our cut-off criteria, a total of 73 trials, or 0.5% of all reaching trials, were removed from analysis. The removed trials reflect reaches that may have been initiated simultaneously with the target coming on (leading to an incorrect ‘start’ position) or trials in which participants aimed in the completely wrong direction, potentially due to a lack of focus. Results do not differ with the inclusion of these trials.

Visuomotor adaptation: rotated reach training trials

Initial analysis established no group differences in PVAE during the Baseline Block of aligned reaching trials early on during reach training (first 15 trials: $F(2,71)=0.619$, $p=0.541$, $\eta^2=0.018$) or at the end of reach training (last 15 trials: $F(2,71)=1.179$, $p=0.314$, $\eta^2=0.033$). Furthermore, there was no Group difference in PVAE in the first block of no-cursor reaches ($F(2,71)=0.813$, $p=0.448$, $\eta^2=0.023$). Thus, our analysis focussed on determining if proprioceptive training influenced visuomotor adaptation. We first analyzed

Fig. 4 Logistic function. A logistic curve was fitted to each participant's percentages of left responses across reference locations to determine their bias (thick dashed black line) and uncertainty range (difference between the thin dotted lines) in each block of proprioceptive training trials. Data are displayed for an example participant, with the white circle indicating body midline. In the inset to the right of the logistic function is an illustration showing the position of body midline (white circle), the participant's bias (black square) seen to be to the left of body midline and uncertainty range (thin lines)



rotated reach training trials early in adaptation (Fig. 2A, B, Box 7). PVAEs were averaged across three consecutive trials for the first 15 rotated reach training trials as follows: average of trials 1–3 (Bin 1), 4–6 (Bin 2), 7–9 (Bin 3), 10–12 (Bin 4), and 13–15 (Bin 5). These values were then normalized by subtracting the average performance on the aligned reach training trials following proprioceptive training or time delay (i.e., Fig. 2A, B, Box 5) using the same sequence of trials just mentioned (i.e., Bins 1–5). To note, only 8 of the 73 excluded trials indicated above fell into the established Bins of 3 reach training trials. All participants had a minimum of 2 reach training trials included per Bin, with data from most participants ($n = 64$) including all 3 trials.

These normalized PVAEs were compared across groups using a 3 Group (PTWF, PTNF, CTRL) \times 5 Bin (Bin 1, Bin 2, Bin 3, Bin 4, Bin 5) mixed ANOVA with RM on the second factor. The magnitude of late visuomotor adaptation observed during rotated reach training was also compared between the 3 Groups (PTWF, PTNF, CTRL), this time using a one-way ANOVA. Late adaptation was considered to be the average PVAE over the last 15 rotated reach training trials, normalized by subtracting the average PVAE of all 15 aligned reach training trials following proprioceptive training or time delay (i.e., Fig. 2A, B, Box 5). The number

of trials included per bin was much less in early versus late reach training (i.e., 3 versus 15 trials), as visuomotor adaptation has been shown to plateau in as little as 10–20 trials (e.g., Zbib et al. 2016; Maksimovic and Cressman 2018), and we wanted to ensure that we captured potential group differences in adaptation. A greater number of trials was used to represent late reach training, after visuomotor adaptation had plateaued, in attempt to minimize variation in reaching errors. In a final analysis, we looked to establish the strength of the group null effects revealed by ANOVA with respect to initial (Bin 1) and late visuomotor adaptation by performing two Bayesian independent samples t tests comparing average PVAE between the PTWF group and the CTRL group during Bin 1 and late adaptation, respectively. The magnitude of the Bayes factor can be interpreted to reflect the strength of support for the null hypothesis (Kelter 2020).

Implicit and explicit visuomotor adaptation: no-cursor reaches

Implicit and explicit contributions to visuomotor adaptation were established using the no-cursor reach training trials. To establish implicit adaptation, we calculated the average PVAE of the 6 exclusion no-cursor reaches immediately

after rotated reach training (i.e., Time 3; Fig. 2A, B, Box 8). This value was taken to be the implicit index according to the following formula:

$$\text{Implicit index (II)} = M_{\text{PV angular error on Exclusion trials}}$$

II values were then normalized by subtracting the average PVAE on the first block of 6 exclusion no-cursor reaches following proprioceptive training or time delay (i.e., Time 2; Fig. 2A, B, Box 6). The extent of implicit adaptation was compared between the 3 Groups (PTWF, PTNF, CTRL) with a one-way ANOVA. To establish explicit adaptation, we calculated the average PVAE of the 6 inclusion no-cursor reaches after rotated reaching (i.e., Time 3; Fig. 2A, B, Box 8) and subtracted the average PVAE of the 6 exclusion no-cursor reaches after rotated reaching (i.e., Time 3; Fig. 2A, B, Box 8), according to the following formula:

$$\text{Explicit index (EI)} = M_{\text{PV angular error on Inclusion trials}} - M_{\text{PV angular error on Exclusion trials}}$$

EI values were normalized by subtracting the average PVAE of the second block of 6 *exclusion* trials following proprioceptive training or time delay (i.e., Time 2; Fig. 2A, B, Box 6). The extent of explicit adaptation was then compared between the 3 Groups (PTWF, PTNF, CTRL) with a one-way ANOVA. Finally, we performed two Bayesian independent samples *t* tests to determine the strength of support for the null hypothesis as revealed by ANOVA with respect to the extent of implicit adaptation and explicit adaptation demonstrated by the PTWF group and the CTRL group.

ANOVAs were conducted in SPSS, following confirmation that data met the assumptions required. When appropriate, the Greenhouse–Geisser correction was applied and corresponding *p* values and effect sizes are reported below. The significance value for all ANOVAs was set at $p < 0.05$, and Bonferroni post hoc tests corrected for multiple comparisons were used to find the locus of significant effects or interactions for all pre-planned comparisons. Bayesian analyses were conducted in JASP.

Results

Proprioceptive training

As shown in Fig. 5A, absolute proprioceptive biases (i.e., response accuracy) improved with proprioceptive training for the PTWF group (Block 1: $M = 2.2^\circ$, $SD = 2.1^\circ$; Block 5: $M = 1.0^\circ$, $SD = 0.9^\circ$). No such improvements were seen in the PTNF group (Block 1: $M = 1.7^\circ$, $SD = 1.3^\circ$; Block 5: $M = 2.5^\circ$, $SD = 1.6^\circ$). ANOVA revealed a significant main effect of Group ($F(1, 46) = 6.784$, $p = 0.012$, $\eta^2 = 0.129$) and a significant Group \times Block interaction ($F(4, 184) = 6.249$, $p = 0.001$, $\eta^2 = 0.120$). The main effect of Block was not significant ($F(4, 184) = 0.771$, $p = 0.508$, $\eta^2 = 0.016$). Pairwise comparisons revealed that biases did not differ between the PTWF and PTNF groups in Block 1 ($p = 0.323$). However, the PTWF group improved with training, such that participants in this group were significantly more accurate at judging the position of their hand in space in Block 3 ($p = 0.049$), Block 4 ($p = 0.045$) and Block 5 ($p = 0.021$) of

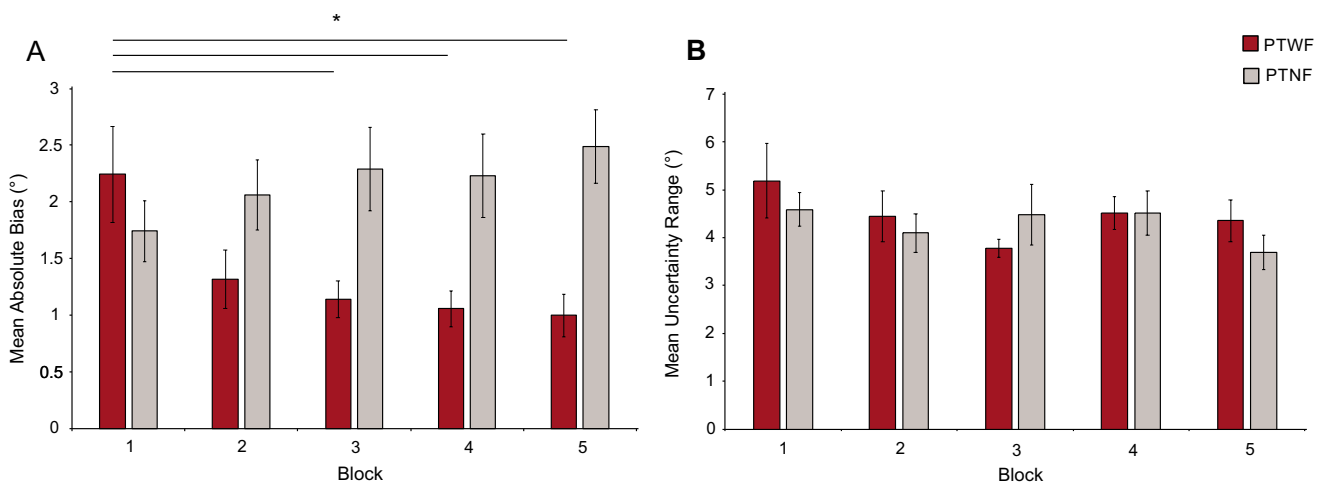


Fig. 5 Proprioceptive acuity. Mean (A): absolute biases (i.e., response accuracy) and (B): uncertainty ranges (i.e., response consistency) across blocks of proprioceptive training (Blocks 1–5) for the Proprioceptive training with feedback (PTWF) group and Proprioceptive training no feedback (PTNF) group. Values closer to zero repre-

sent greater accuracy and consistency. Red and light gray bars represent proprioceptive performance for the PTWF group and the PTNF group, respectively. Error bars represent group standard error of the mean. The asterisk (*) indicates a significant difference between Blocks 3, 4, and 5 compared to Block 1 for the PTWF group

proprioceptive training compared to Block 1. Biases did not change across blocks of training for the PTNF group, such that no two blocks differed from each other (all $p > 0.57$). Indeed, by Block 5, proprioceptive biases were significantly more accurate for the PTWF group compared to the PTNF group ($p < 0.001$).

In Fig. 5B, we display the mean uncertainty ranges (i.e., response consistency) for the PTWF and PTNF groups across proprioceptive training blocks. ANOVA revealed no significant main effects (Group: $F(1, 46) = 0.121$, $p = 0.730$, $\eta^2 = 0.003$; Block: $F(4, 184) = 2.105$, $p = 0.103$, $\eta^2 = 0.044$), and no significant Group \times Block interaction ($F(4, 184) = 1.399$, $p = 0.246$, $\eta^2 = 0.030$). As seen in Fig. 4B, uncertainty ranges did not significantly change across blocks of training for the PTWF group (Block 1: $M = 5.2^\circ$, $SD = 3.8^\circ$; Block 5: $M = 4.4^\circ$, $SD = 2.1^\circ$) or the PTNF group (Block 1: $M = 4.6^\circ$, $SD = 1.7^\circ$; Block 5: $M = 3.7^\circ$, $SD = 1.7^\circ$).

Visuomotor adaptation: rotated reach training trials

Figure 6 shows the extent of visuomotor adaptation at the start of rotated reach training (i.e., first 15 trials; average of every 3 trials (Bins 1–5)) and at the end of rotated reach training (i.e., last 15 trials) for all groups. Groups adapted their reaches as training continued across Bins ($F(4, 276) = 123.351$, $p < 0.001$, $\eta^2 = 0.641$), such that PVAE of the hand achieved in Bin 5 was significantly greater than PVAE achieved in the first 3 Bins (all $p < 0.001$). ANOVA revealed that the Groups did not significantly differ with respect to the magnitude of visuomotor adaptation early in training (Group: $F(2, 69) = 0.816$, $p = 0.446$, $\eta^2 = 0.023$;

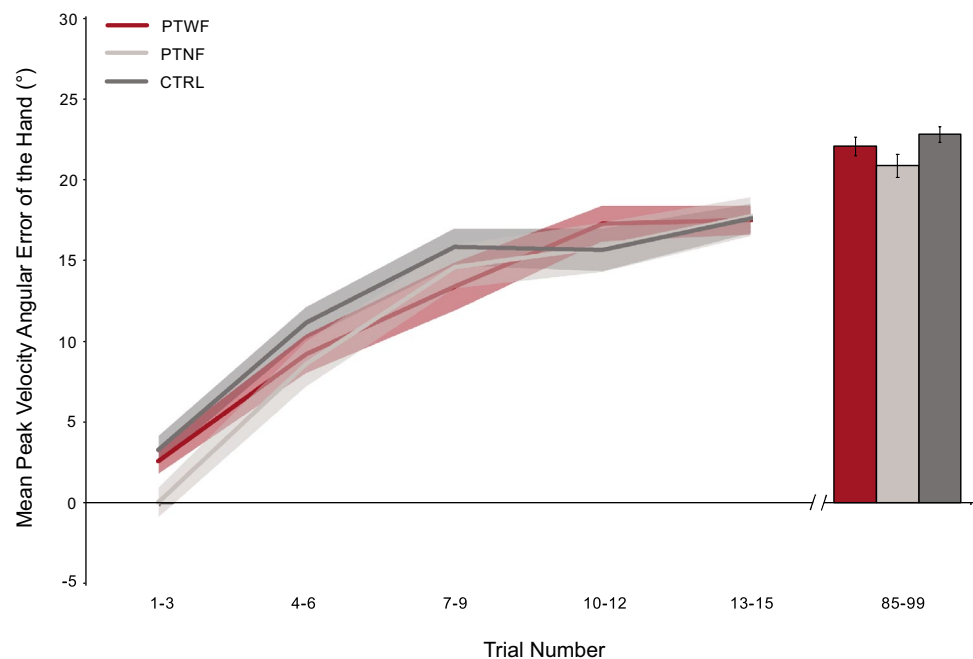
Group \times Bin interaction: $F(8, 276) = 1.206$, $p = 0.299$, $\eta^2 = 0.034$). As revealed by a moderate effect (Kelter 2020), Bayesian analysis further indicated that the PTWF group and CTRL group demonstrated a similar extent of visuomotor adaptation initially (Bin 1) when first learning to reach with a rotated cursor ($BF_{01} = 2.951$).

Late in rotated reach training, participants achieved an average PVAE of 21.9° , which did not differ between Groups ($F(2, 71) = 2.622$, $p = 0.080$, $\eta^2 = 0.066$). That said, there was a trend for the PTNF group ($M = 20.9^\circ$, $SD = 3.6^\circ$) to display less changes in their reaches compared to the PTWF group ($M = 22.1^\circ$, $SD = 2.8^\circ$) and the CTRL group ($M = 22.8^\circ$, $SD = 2.5^\circ$). Again, results from our Bayesian analysis supported the conclusion that the PTWF group and CTRL group demonstrated a similar magnitude of visuomotor adaptation at the end of rotated reach training ($BF_{01} = 2.340$).

Implicit and explicit visuomotor adaptation: no-cursor reaches

The extent of implicit and explicit adaptation following rotated reach training are shown in Fig. 7A and B, respectively. With respect to implicit adaptation, ANOVA revealed a significant main effect of Group ($F(2, 71) = 3.149$, $p = 0.049$, $\eta^2 = 0.077$). Post hoc analysis revealed that the PTNF group ($M = 9.1^\circ$, $SD = 4.5^\circ$) demonstrated significantly less implicit adaptation compared to the CTRL group ($M = 12.8^\circ$, $SD = 4.2^\circ$) ($p = 0.048$). Implicit adaptation for the PTWF group ($M = 11.5^\circ$, $SD = 6.5^\circ$) did not differ significantly from the PTNF group ($p = 0.319$) or the CTRL group ($p = 1.000$). As revealed by a moderate

Fig. 6 Visuomotor adaptation. Mean peak velocity angular error (PVAE) of the hand for all three groups of participants (Proprioceptive training with feedback (PTWF; red), Proprioceptive training no feedback (PTNF; light gray), and Control (CTRL; dark gray)) when adapting to a 30° clockwise cursor rotation. Normalized data is presented at the start of rotated reach training trials (average of three consecutive trials for trials 1–15) and at the end of rotated reaching training (average of last 15 trials). Positive values indicate reaching to the left of the target, and negative values indicate reaching to the right of the target. Shaded regions and error bars represent group standard error of the mean



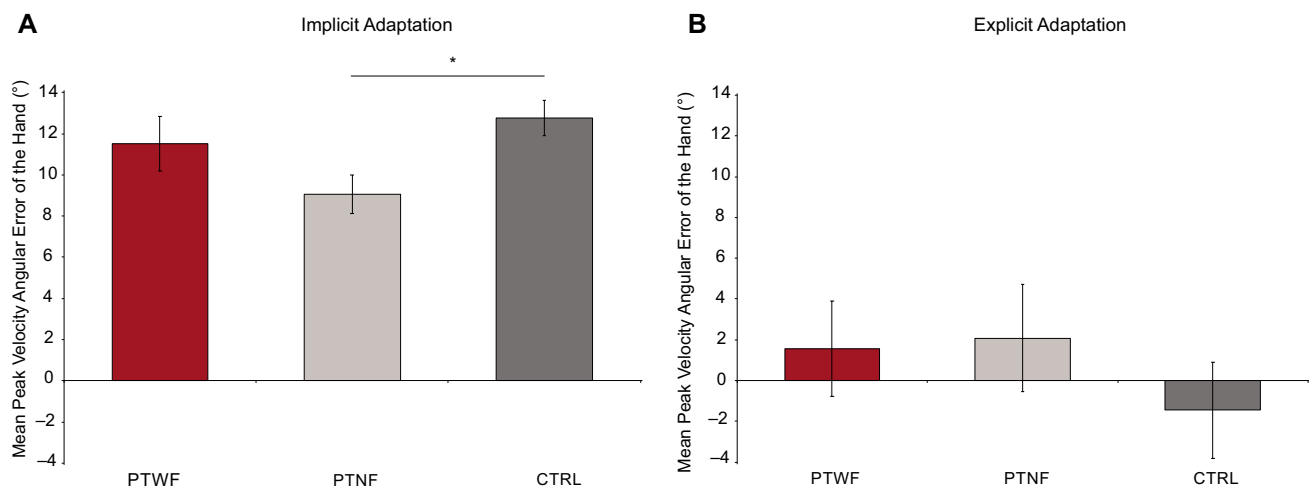


Fig. 7 Implicit and explicit adaptation. Normalized mean (**A**): implicit adaptation and (**B**): explicit adaptation for all three groups of participants (Proprioceptive training with feedback (PTWF; red), Proprioceptive training no feedback (PTNF; light gray), and Control (CTRL; dark gray)), where positive values indicate reaching to the

left of the target, and negative values indicate reaching to the right of the target. Error bars represent group standard error of the mean. The asterisk (*) indicates a significant difference between the PTNF group and CTRL group

effect, Bayesian analysis suggested that the PTWF group and CTRL group demonstrated similar implicit visuomotor adaptation ($BF_{01} = 2.707$).

With respect to explicit adaptation, ANOVA revealed no significant difference between Groups ($F(2, 71) = 0.612$, $p = 0.545$, $\eta^2 = 0.017$), such that the PTWF group ($M = 1.6^\circ$, $SD = 11.4^\circ$), PTNF group ($M = 2.1^\circ$, $SD = 12.8^\circ$) and CTRL group ($M = -1.5^\circ$, $SD = 11.6^\circ$) all demonstrated minimal explicit adaptation. Finally, Bayesian analysis indicated that the PTWF group and CTRL group demonstrated similar explicit visuomotor adaptation ($BF_{01} = 2.487$).

Discussion

In the current experiment, we tested the influence of proprioceptive training on visuomotor adaptation to establish if improving proprioceptive acuity leads to benefits in visuomotor adaptation. Two groups of participants completed proprioceptive training, where their hand was passively moved to an unseen reference location and they indicated the position of their felt hand on every trial. In accordance with the methodology of McGregor et al. (2018), one group was provided with feedback regarding their response accuracy on the middle 60% of proprioceptive training trials (PTWF), while the other group did not receive any feedback during training (PTNF). Providing feedback on only the middle 60% of proprioceptive training trials for the PTWF group, enabled us to establish persistent changes in proprioceptive acuity in the absence of feedback, as well as assess proprioceptive acuity in the PTWF and PTNF groups under similar

conditions (i.e., proprioceptive acuity in the first versus the last block of proprioceptive training trials). A third control group (CTRL) was included in our study, but did not participate in proprioceptive training and instead sat quietly during this training time. We found that proprioceptive training with feedback led to improved proprioceptive acuity, such that the PTWF group decreased their proprioceptive biases (i.e., improved their ability to accurately locate the position of their hand in space) over the blocks of proprioceptive training trials. That said, we found no benefit of proprioceptive training on visuomotor adaptation, either at the start or at the end of rotated reach training. Specifically, all three groups showed a similar magnitude of visuomotor adaptation across the rotated reach training trials. As well, as seen in Fig. 7, visuomotor adaptation was primarily driven by implicit processes for all groups, and the magnitude of implicit and explicit adaptation did not vary significantly between the PTNF and CTRL groups compared to the PTWF group. The lack of group differences was supported by our large sample size in comparison to previous work (e.g., the current experiment had 24 participants per group in comparison to the 14 participants per group of Darainy et al. (2013)).

Proprioceptive training

Early proprioceptive training regimes have been successful in improving tactile sense and proprioceptive acuity of the upper limb in post-stroke individuals (Carey et al. 1993, 1995, 1996, 1997, 2000, 2002). This training has included patients identifying different tactile surfaces and providing judgments of felt limb position following

passive movements to unknown locations. More recently, the benefits of proprioceptive training using a hand positioning task have been examined in healthy participants (Darainy et al. 2013; McGregor et al. 2018). Within the hand positioning task, participants grasp a robot handle and their hand is passively moved to an unknown reference location. Participants then judge their hand's final location relative to their body midline, and verbal feedback regarding the accuracy of their response may or may not be provided. Using this proprioceptive training regime, Darainy et al. (2013) and McGregor et al. (2018) have demonstrated that healthy individuals are able to improve their proprioceptive acuity following training when feedback is provided, such that they become more accurate at locating the position of their hand in space (Darainy et al. 2013; see also McGregor et al. 2018).

In our study, we adopted the proprioceptive training protocol used by Darainy et al. (2013) and McGregor et al. (2018) and found that proprioceptive acuity improved for the group that received feedback regarding response accuracy during training. Specifically, the PTWF group demonstrated enhanced proprioceptive accuracy by the end of the proprioceptive training blocks such that biases decreased by 1.24° (equivalent to 0.33 cm) from the first to the last block of proprioceptive training. This improvement in proprioceptive biases is similar to the 0.34 cm improvement reported by Darainy et al. (2013). In contrast, we did not see a similar improvement in response accuracy for our PTNF group, whose proprioceptive biases did not differ significantly across Blocks. Also important to note is that we did not find any significant changes when it came to response consistency (i.e., magnitude of uncertainty ranges) for either the PTWF or PTNF groups.

Similar to previous studies (e.g., Darainy et al. 2013; see also McGregor et al. 2018), we discuss improvements in participants' biases as reflecting enhanced accuracy in judging felt hand position. Alternatively, improvements in participants' biases may reflect greater sensitivity to initial hand motion, as participants could base their judgments of final hand position on the remembered direction of hand motion. On all proprioceptive training trials, participants knew that they would be making a judgment of their hand position relative to their body midline. Our current paradigm does not allow us to dissociate whether proprioceptive training with feedback in our PTWF group lead to enhanced accuracy in judging perceived felt hand position or hand motion. That said, it is evident that proprioceptive training led to improved proprioceptive acuity in our PTWF group. We now examine if this improved proprioceptive acuity benefitted visuomotor adaptation.

Proprioceptive training and motor learning

In contrast to our expectations, we found no benefit of proprioceptive training on visuomotor adaptation in the current study. While participants in our PTWF group improved their proprioceptive acuity with training, this enhanced proprioceptive acuity did not lead to benefits in early or late visuomotor adaptation when compared to our PTNF group or CTRL group. In contrast, similar proprioceptive training protocols with feedback have been shown to benefit motor adaptation to a velocity-dependent forcefield. Specifically, participants adapted their reaches earlier (i.e., had less curved trajectories) when introduced to a velocity-dependent forcefield following proprioceptive training compared to participants who did not receive feedback during proprioceptive training or did not complete the proprioceptive training at all (Darainy et al. 2013; McGregor et al. 2018).

We suggest that the lack of benefits observed in our visuomotor adaptation paradigm compared to previous forcefield adaptation paradigms may arise due to the different error signals present within the two paradigms. Reaching in a velocity-dependent forcefield generates a sensory prediction error signal, as the predicted sensory (visual and proprioceptive) consequences of one's movement do not match the actual sensory feedback experienced during movement (Tseng et al. 2007; Sarlegna and Bernier 2010; Shadmehr et al. 2010). To resolve this error signal, the internal model for reaching is updated to allow the movement to be carried out as desired, where the internal model consists of the inverse model (i.e., motor command) and the forward model (i.e., expected sensory consequences of executing the (adapted) motor command; Wolpert et al. 1995; Shadmehr et al. 2010).

Similar to forcefield adaptation paradigms, visuomotor adaptation paradigms also give rise to a sensory prediction error signal, as the expected (visual) position of the cursor does not match the seen position of the cursor while reaching. Visuomotor adaptation paradigms further introduce a cross-sensory error signal, due to the sensory discrepancy between one's visual estimate of hand position (i.e., seen position of the cursor) and proprioceptive estimate of hand position (i.e., felt hand position; Cressman and Henriques 2009; Salomonczyk et al. 2013; Maksimovic et al. 2020). To resolve this cross-sensory error signal, it has been shown that we recalibrate our sense of felt hand position (i.e., proprioception) in order to match the visual information provided (Cressman and Henriques 2009, 2010; Salomonczyk et al. 2011, 2012, 2013; Mostafa et al. 2014). Specifically, one shifts their felt hand location in space so that it is more aligned with the cursor feedback provided. Cressman and Henriques (2010) have further shown that, when only the cross-sensory error signal is present (i.e., the hand is passively moved and no sensory prediction error signal is

experienced), the extent of proprioceptive recalibration and visuomotor adaptation are similar in magnitude and significantly correlated. From these results, Cressman and Henriques (2010) concluded that proprioceptive recalibration contributes to visuomotor adaptation.

While proprioceptive processing has been implicated in visuomotor adaptation, our current results suggest that improving the accuracy of this sense does not benefit visuomotor adaptation, nor does proprioceptive training prime cortical somatosensory and motor areas for adaptation in the same manner as suggested for forcefield adaptation (McGregor et al. 2018). The lack of differences in visuomotor adaptation with varying levels of proprioceptive acuity has been demonstrated by Cressman and colleagues (2010, 2021). In 2010, Cressman et al. looked to determine if healthy young and older adults demonstrated a similar magnitude of proprioceptive recalibration and resulting visuomotor adaptation, while in 2021, Cressman and colleagues compared visuomotor adaptation in individuals with Parkinson's disease (PD) and age-matched healthy control participants. The authors hypothesized that older adults and individuals with PD would recalibrate proprioception to a greater extent than their control counterparts due to age and disease related deteriorations in proprioceptive acuity, respectively (Cressman et al. 2010; Cressman et al. 2021), and hence show greater visuomotor adaptation. Contrary to their expectations, Cressman and colleagues found no differences in proprioceptive recalibration and a similar extent of visuomotor adaptation across young and older participants (2010), and across patients with PD and healthy control participants (2021).

Given that proprioceptive accuracy does not appear to impact visuomotor adaptation, one may ask how proprioception and proprioceptive recalibration are implicated in visuomotor adaptation. Early work has demonstrated that visuomotor adaptation can arise in the absence of proprioception (i.e., in a deafferented individual; Lajoie et al. 1992; Ingram et al. 2000; Bernier et al. 2006), when there is no cross-sensory error signal, and vision alone drives adaptation. Findings by Bernier and colleagues (2009) further reveal that healthy individuals suppress proprioceptive input when initially introduced to the visuomotor distortion. In their paradigm, Bernier and colleagues (2009) measured sensory evoked potentials in response to median nerve stimulation at the wrist of the moving hand over the course of visuomotor adaptation. They found that for the first few trials, participants who demonstrated the greatest sensory suppression (i.e., had the smallest sensory evoked potentials) adapted their reaches to a greater extent, such that their movements were straighter with fewer corrections compared to participants who had larger sensory evoked potentials. As all participants gradually adapted their reaches, sensory evoked potentials increased in magnitude, indicating that

proprioception was processed to a greater extent (Bernier et al. 2009). This increase in sensory processing with time may correspond to when participants recalibrated proprioception, as Zbib et al. (2016) have shown that proprioception takes time to be significantly recalibrated (~ 70 trials).

Alternatively, the increased processing of proprioceptive information with time may reflect modifications in the weighting of sensory signals (Smeets et al. 2006). Smeets et al. (2006) suggest that visual and proprioceptive signals are not mutually calibrated, but instead sensory signals are integrated in an optimal manner when one has to reach to a target (e.g., van Beers et al. 1996, 1998). The conclusions drawn by Smeets et al. (2006) regarding sensory re-weighting arise from reaching errors observed when the availability of aligned visual feedback was manipulated. According to Redding and Wallace (1996, 1997), for recalibration between vision and proprioception to occur, the two signals must be misaligned. In agreement with this proposal and similar to the suggestions of Smeets and colleagues, we have shown that proprioception is not recalibrated after participants reach with aligned cursor feedback (see Cressman and Henriques 2009, and Jones et al. 2009).

The contributions of proprioceptive recalibration and sensory re-weighting to changes in proprioceptive processing over time, and hence visuomotor adaptation, remain to be determined. That said, the results from the current study suggest that the accuracy of one's proprioceptive sense does not impact visuomotor adaptation. Specifically, we show no benefit and no cost of proprioceptive training on visuomotor adaptation, as participants in the PTWF group performed similarly to those in the PTNF and CTRL groups. We suggest that this lack of influence of proprioceptive training on visuomotor distortion may arise due to the flexibility in the extent that proprioception is processed during initial visuomotor adaptation (i.e., proprioceptive input is ignored during initial visuomotor adaptation).

Mechanisms underlying visuomotor adaptation

It has been suggested that motor adaptation arises implicitly (unconsciously) when adapting to both forcefield (Donchin et al. 2003; Ostry et al. 2010) and visuomotor distortions (Wolpert et al. 1995; Shadmehr et al. 2010). Particularly, when reaching with a small visuomotor distortion (less than, or equal to, 30°), it has been shown that visuomotor adaptation is primarily driven by implicit processes (Werner et al. 2015; Neville and Cressman 2018; Modchalingam et al. 2019). When reaching with a small distortion, participants experience a small target error, and as a result, do not become aware that the reaching environment has changed or that they have changed their movements (i.e., participants are unable to report the presence of a visuomotor distortion,

or indicate strategic changes in their reaches that they have adopted).

To determine the underlying contributions of implicit and explicit processes to visuomotor adaptation in the current paradigm and if these were influenced by proprioceptive training, we had participants reach in the absence of cursor feedback when provided with the following instructions: (1) “Reach so that your hand goes straight to the target” and (2) “Reach using anything you have learned during training in order to get the cursor to the target”. These instructions were first used in the visuomotor adaptation literature by Werner et al. (2015), and are adopted from the Process Dissociation Procedure put forth by Jacoby (1991). When adopting this procedure, one assumes that participants are able to consciously engage and disengage from a learned reaching strategy when instructed to do so. Moreover, the paradigm assumes that the implicit processes engaged do not differ between the two sets of trials, an assumption that has been questioned by Heuer and Hegele (2015). Keeping these limitations in mind, and the fact that implicit adaptation has been shown to decay quickly in comparison to explicit adaptation (see Neville and Cressman 2018; Bouchard and Cressman 2021; Heirani Moghaddam et al. 2021), our participants always completed reaches under the first set of instructions (i.e., reach directly to the target), before they were cued to the presence of the visuomotor distortion by asking them to reach with any learned strategy. Future research is required to establish the relationship between implicit and explicit adaptation processes engaged and how they differ depending on assessment method (see Heirani Moghaddam et al. 2021, 2022).

Using the Process Dissociation Procedure, we found that even when participants were instructed to aim directly to the target, they reached to the left of the target, demonstrating implicit adaptation of 11.1° (see Fig. 7A). Participants then continued to reach in a similar manner, even when asked to reach using any learned strategy in order to get the cursor to the target, thus demonstrating minimal explicit adaptation. In fact, explicit adaptation was only 0.7° on average across all participants, and did not differ from baseline performance.

Implicit adaptation was observed across all 3 groups of participants. Surprisingly, we found that the PTNF group displayed significantly less implicit adaptation (9.1°) compared to the CTRL group (12.8°). At present, it is unclear how to account for this finding and future work is required to determine the impact that (1) passively moving one’s hand in directions that are not related to the upcoming goal movement, and (2) having participants provide prolonged judgments of hand position in the absence of feedback, have on the processes underlying visuomotor adaptation.

In contrast to the group differences observed with the PTNF and CTRL groups, implicit adaptation observed in

the PTWF group (11.5°) did not differ significantly from the other two groups. While group differences with respect to implicit adaptation were not observed in reference to the PTWF group, we acknowledge that participants performed only a limited number of no-cursor reaches to determine implicit and explicit adaptation as established using the Process Dissociation Procedure. If changes in how proprioception is processed over trials (due to proprioceptive recalibration and/or sensory re-weighting) play a role in visuomotor adaptation, group differences may have emerged if additional trials were included.

Conclusion

Proprioceptive training has been shown to improve proprioceptive acuity, and benefit motor adaptation when reaching in a velocity-dependent forcefield. Here, we asked if similar benefits are present when reaching with a visuomotor distortion. Additionally, we asked if these benefits would arise implicitly or explicitly. We found that proprioceptive training improved participant’s proprioceptive acuity when feedback regarding response accuracy was provided. While proprioceptive acuity improved with proprioceptive training, this did not influence early or late visuomotor adaptation, which was shown to arise implicitly. Thus, we conclude that improving proprioceptive acuity does not benefit, nor hinder, implicit visuomotor adaptation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00221-022-06352-4>.

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Data availability Data that support the findings of this study are available as a Supplementary File.

Declarations

Conflict of interest The authors have no conflicts to disclose.

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