EFFECTS OF TOOL USE AND PERTURBATION DURING MOTOR ADAPTATION ON HAND LOCALIZATION IN IMMERSIVE VIRTUAL REALITY

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Abstract

Our brain has a remarkable capacity for learning movements and adapting them to accomplish a motor goal. In many adaptation studies, participants move in a 2D plane while their hand is represented by a cursor. When visual feedback of hand position is misaligned, people can quickly compensate for this perturbation, show persistent reach aftereffects, and even misestimate the location of the unseen hand in the direction of previous visual training. However, it is unknown how well this generalizes to real-world settings or to the tools we use every day. Immersive virtual reality was used to test if end-effector shifts are also observed in more naturalistic virtual reality environments and if they extend to tools as end effectors.

In the Hand Experiment, previous work from our lab was replicated where we found shifts in end-effector localization after adapting reach movements to a 30° and 60° visuomotor rotation of the hand, showing a similar magnitude of both shifts in where people indicate their perceived/felt hand and reach aftereffects following training to the perturbation in the VR environment. In the Pen Experiment, this paradigm was extended to investigate how well people can adapt when aiming with a common tool, like a pen, and whether the tool location is also recalibrated. The extent that the unseen location of hand-held tool, as well as the hand (in separate trials) recalibrates with adaptation was measured. Our results provide insight into the adaptative processes involved when learning to wield tools in more complicated, realistic environments.

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General Introduction and Literature Review

Humans constantly need to adjust their movements to cope with changes, whether external, like using a new tool or moving underwater, or internal, such as dealing with injury or fatigue. This adjustment process, known as motor adaptation, involves modifying well-practiced actions to maintain performance in a changing environment (Krakauer et al., 2019). Modern technologies have intensified the demand on the motor system to adapt and switch between different learned visuomotor mappings, which link vision and movement.

Motor adaptation

Motor adaptation refers to the process by which the motor system adjusts to changes in the environment or body, allowing for accurate movements despite perturbations. This form of short-term motor learning occurs over minutes to hours, making it more easily studied than long-term skill acquisition. Motor adaptation is largely an implicit or unconscious process. A specific type of motor adaptation, visuomotor adaptation, involves adjusting reaching movement in response to altered visual feedback of the hand (Krakauer et al., 2019). Specifically, the visual feedback of the hand's position (typically represented by a cursor) is rotated by a predetermined angle relative to the starting position. During visuomotor adaptation, we experience a sensory-motor mismatch between the actual hand movement and its visual representation, prompting adaptive motor responses (Krakauer et al., 2019; Block & Lui, 2023). Our brain detects this mismatch between the intended and actual outcome and gradually adjusts motor commands to reduce this discrepancy. This is illustrated in Figure 1 where a blue cursor represents the hidden hand position. In the right panel, the cursor path is rotated 30° left of the target and to counter this perturbation, participants need to move their hand 30° right to acquire the target. Normally, only about 20 trials of practice is required with this consistent rotation, for a single target or a set of neighbouring targets, in order compensate for this perturbation (Krakauer et al., 2020).

Following visuomotor adaptation, even after perturbation is removed, people continue to demonstrate deviations in reaching movements they exhibited during adaptation to the rotated hand-cursor. This is known as reach after-effects (Gastrock et al., 2020; Modchalingam et al., 2019; Ong & Hodges, 2010; Fernandez-Ruiz et al., 2010). These reach aftereffects persist even when participants are informed that the perturbation has been removed and are instructed to disengage any conscious strategies. As a result, reach aftereffects are considered an implicit measure of motor adaptation. They are usually capped at approximately 15 degrees, regardless of the magnitude of the visuomotor rotation or misalignment (Gastrock et al., 2020; Modchalingam et al., 2019; Bond & Taylor, 2015). This consistent upper limit suggests a saturation point in the implicit adaptation process. As the motor system gradually readjusts to normal visuomotor mapping, reach aftereffects decay over time in the absence of perturbed feedback. Understanding the characteristics of reach aftereffects provides valuable insights into the mechanisms underlying motor adaptation and the brain's ability to recalibrate sensorimotor relationships.

Estimating and updating hand position

Our ability to estimate limb position is crucial for planning, executing, and adjusting goal-directed movements. This estimation relies on multiple sources of information, primarily visual and somatosensory signals (from receptors in muscles, joints, and skin). Additionally, efferent signals or efference copies—neural duplicates of motor commands— are used by other regions in the brain to interpret and predict sensory consequences of impending actions. These diverse inputs collectively form an internal representation of limb position, enabling the nervous system to differentiate between self-generated and external stimuli, facilitate smooth movements, and implement rapid error corrections. This multifaceted sensory integration allows for precise motor control and adaptation in various environmental contexts ('t Hart & Henriques, 2016; Mostafa et al., 2019).

Estimates of limb position are not only necessary for planning, producing and adapting movements, but these estimates are in turn somewhat plastic, especially in the face of altered visual feedback. Specifically, people’s perceived location of their unseen hand changes after training with altered visual feedback of the hand (Tsay et al., 2022; Gastrock et al., 2020;

Modchalingam et al., 2019; Izawa et al., 2012; Ruttle et al., 2021; Rand & Heur, 2019), as well as when adapting to dynamics perturbations (Ostry et al., 2010; Ohashi et al., 2019). In visuomotor rotation studies, in the absence of any visual feedback, the perceived hand location shifts towards the perturbed cursor experienced during training (Tsay et al., 2022; Gastrock et al., 2020; Modchalingam et al., 2019; Izawa et al., 2012; Ruttle et al., 2021; Rand & Heur, 2019). Similar to reach aftereffects, shifts in hand position estimates are generally robust but are typically limited to approximately 6 degrees, independent of the size of the visuomotor perturbation (Modchalingam et al., 2019). While the magnitude of this proprioceptive recalibration is smaller than of reach aftereffects, they are moderately correlated with reach aftereffects (Modchalingam et al., 2019; Gastrock et al., 2010; Ruttle et al., 2021). Additionally, as with reach aftereffects, adjustments in the perception of an unseen hand—especially those related to proprioceptive recalibration—can still occur even when individuals are aware of the discrepancy between the hand-cursor alignment and their actual hand position. (Gastrock et al., 2020; Modchalingam et al., 2019). Even though motor aftereffects and shifts in estimates of hand location are implicit, they emerge quickly requiring only a dozen or so trials to saturate (Ruttle et al., 2022; Zbib et al., 2016). This suggests that these shifts in proprioceptive estimates are not merely a by-product of learning but could be contributing to reach adaptation from the onset.

The changes in perceived hand position during adaptation likely reflects updates in both afferent and efferent based estimates. In studies where people estimate their unseen hand location after they generated their own hand movement to a location of their choice (active hand localization) or when their hand is passively moved by a robot (passive hand localization), we find that the learning-induced shift is 5-10% larger when the hand movement is self-generated during hand localization trials compared to when the hand is passively placed ('t Hart &

Henriques, 2016; Gastrock et al., 2020; Modchalingam et al., 2019). However, given that active hand localization reflects both proprioception and efferent based estimates, this suggests that most of the shift in hand localization following training reflects proprioceptive recalibration (Gastrock et al., 2020; Modchalingam et al., 2019; 't Hart & Henriques, 2016; Mostafa et al., 2019; Ruttle et al., 2021). Our study employs active hand movements, a common approach in similar paradigms that eliminates the need for robotic devices. While this allows us to assess shifts in end-effector localization following training with rotated feedback without a robotic device, we cannot separate out contributions from efferent and afferent signals in our current study. Nevertheless, we can assess end-effector localization shifts in virtual reality (VR), along with reach adaptation and aftereffects.

Immersive VR is being increasingly used for motor learning and rehabilitation (Carter et al., 2016; Anglin et al., 2017; Juliano et al., 2022). Just as observed in conventional visuomotor adaptation paradigms, adaptation in VR has also shown that participants compensate for reaches and show persistent reach aftereffects (Carter et al., 2016). Increased motivation and engagement in VR rehabilitation interventions could lead to better outcomes since patients would be more motivated to perform the tasks. VR is also a safe and cost-effective way to replicate real-world scenarios within a controlled environment (Carter et al., 2016; Anglin et al., 2017; Alzayat et al., 2019; Juliano et al., 2022). However, research has shown that immersive VR requires greater cognitive processing compared to conventional environments, therefore increasing cognitive load which could prolong the adaptation process (Juliano et al., 2022). Others suggest that in visuomotor adaptation, participants adapt similarly in both VR and conventional environments, with VR increasing cognitive load (Anglin et al., 2017). As a result, this study will also provide insight into visuomotor adaptation using a VR paradigm.

Such changes in goal-directed movement and perceived hand localization have been observed in experimental settings where participants are required to move a cursor (representing their unseen hand) to a target on a two-dimensional display. However, it remains unclear whether these sensory and motor adjustments also occur with the tools we use in everyday life. This study aims to address this gap by investigating whether end-effector shifts—similar to those observed in traditional experiments—also occur in VR environments. Additionally, we will explore if these shifts extend to interactions with tools as end-effectors, providing insight into how these phenomena translate to real-world applications and tool use.

Tool use

Humans can make very specific adjustments with their hands such as grasping a tool and then manipulate that tool for varying purposes. For example, when playing a sport such as baseball, the player can estimate the trajectory of a swing by adjusting their body in a way that fits the bat and consequently, are able to hit the ball since they are able to embody the bat as if it was as extension of their hand. In humans, the use of tools is facilitated by tool embodiment where the tool is integrated into our body schema (Bell et al., 2022). The tool produces a specific perceptual change of the body representation where the tool is an extension of the body and the visual receptive fields are projected out to the tool (Bell et al., 2022). Peripersonal space consists of fields near the body where multisensory information is incorporated, allowing the brain to predict interactions between the body and other stimuli in the environment (Weser & Proffitt, 2021). The intraparietal cortex contains two important neurons: distal type responds to stimuli on and near the hand and proximal type responds to stimuli on the shoulder, neck, and in space (Maravita & Iriki, 2004). It has been shown that after training to obtain food using a tool, the distal and proximal type neurons expand their response to include the tool and its surrounding area (Maravita & Iriki, 2004). Peripersonal space highlights areas of the environment that are relevant to the movement of the tool by updating perception of space after tool use (Bell et al., 2022). In motor adaptation studies, participants learn to change their hand direction or extent of movement, resembling certain aspects of tool use such as the distance between hand and tip of the tool. Therefore, we would expect that participants who use a tool to reach to targets should also show motor adaptation, just as in experiments performed with a hand (Alzayat et al., 2019).

For the purposes of this study, we used a common tool that is used on a daily basis and comes in a standard shape – a pen. Since the study was performed in an academic environment, we chose a standard York University pen. Due to extensive use, participants are not required to familiarize themselves with how to wield pens since university students use them very frequently, unlike most tools used in sports and other domains. Thus, we could focus on how well people adapt to altered visual feedback of the pen motion and whether this changes people's estimate of the unseen pen.

Research Question

In the first part of the study, we will replicate previous work from our lab where we found shifts in end-effector localization after adapting to a 30° and 60° visuomotor rotation of the hand using a cursor on a 2-D screen (Modchalingam et al., 2019; Gastrock et al., 2020). In the second part of the study, we will investigate how well people can adapt when acquiring the target with a tool used in our daily lives, like a pen, and test whether tool location is also recalibrated. Participants will acquire the target using a virtual pen whose pen-tip movements will also deviate by 30°: tool tip rotation adaptation. Then we will measure the extent that the unseen location of the tool-tip and hand (in separate trials) recalibrates with tool-tip adaptation. Our results will provide insight into the adaptative processes involved when learning to wield tools in a VR environment and will further increase our understanding of proprioceptive recalibration.

Methods

Participants

This study had a within-subjects design, allowing for repeated-measures across the three experimental groups. Twenty-five students (19 females, $M_{\text{Age}} = 23.6$, $SD = 8.98$) participated in the 30° hand experiment. Thirty-eight students (26 females, $M_{\text{Age}} = 20.5$, $SD = 2.05$) participated the 60° hand experiment and 30° pen experiment. Across the experiments, participants overlapped but were tested months apart before participating in each of the experiments on measures that would not be retained. Participants were recruited from York University to perform reach tasks. All participants reported having normal or corrected to normal vision, and gave prior, written, informed consent. Nearly all participants were right-handed, except for two that were left-handed and one ambidextrous in the 60° hand experiment and 30° pen experiment. Procedures to be used in this study were approved by York University's Human Participants Review Subcommittee.

Experimental set-up

Apparatus

Participants sat on a height-adjustable chair facing a table that was at waist level. They put on a head-mounted display system (HMD: Oculus Rift Consumer Version 1; resolution 1080 by 1200 for each eye; refresh rate 90 Hz for each eye) and held an Oculus Touch controller in each hand.

All visual feedback was provided through the HMD in an immersive VR experiment space developed in Unity 3D with a sampling rate of about 70 Hz. We used the Unity Experiment Framework to manage trial and block schedules within the experiment (Brookes et al., 2020). Three Oculus Constellation sensors were used to increase spatial resolution and tracked the position of the headset and controllers. The positional data was obtained from the Meta software. For setups similar to the one used in this study, positional accuracy would be within millimeters with errors in the non-vertical dimensions expected to be less than 1% for the movement size used in this study (Borrego et al., 2018; Shum et al., 2019).

Participants were instructed to face forward and slightly tilted their head down to see the stimuli. At the beginning of the experiment, the experimenter pressed a button to center the visual stimuli around the location of the right-hand controller of the participant at the physical docking station, which was located at the edge of table just in front the body, along the midline. A magnet was mounted at the dock for participants to place their controller back at the start of each trial. From there, participants moved out their hand-held controller to a common home start position, then target (Figure 1) or an arc (Figure 2) depending on the task, as described below. A trial board showed participants the remaining number of trials. Participants smoothly glided their arm along the table to reach to the targets. They were instructed to make straight, smooth, and accurate reaches to the target. Although there was no strict time limits imposed, the experimenter encouraged participants to move to the target in a fast and uniform pace. Here, we use a main measure in our field for measuring adaptation and usually reaction times and movement times do not reflect changes in adaptation. While it is possible, in this study we should not see a difference in movement time as it is not a reliable measure of learning (Gastrock et al., 2024).

The study consisted of two experiments in immersive VR. The Hand Experiment acted as a baseline by having participants acquire the target using their right thumb, which was represented by a blue cursor, as shown in Figure 2. In the Pen Experiment, participants acquired the target using the tip of a virtual pen, while also having a physical pen secured onto the controller. The physical pen was secured on to the right controller so that participants kept their right thumb on the pen throughout the experiment. The physical pen provided the participant with tactile information with the intention of making the experiment feel more realistic. The visual apparatus in the second experiment was the same as the Hand Experiment, except the scene was an office setting rather than a room, the table surface was replaced with that of an office desk, and reaches were performed using the tip of the pen rather than a cursor.

Hand Experiment

Reach to Target tasks. At the beginning of each block of trials, 'Reach to Target' was displayed on the screen. Afterwards, the participants kept a cursor (blue sphere, 1 cm diameter) representing their right index finger at the home position for 300 ms, so that a target (red sphere, 1 cm diameter) could appear at one of four possible locations (as shown in Fig. 1). The targets were located 12 cm away from the home position and were positioned either straight ahead at 90°, to the right at 70°, or to the left at 110° and 130° in polar coordinates on a table with a dark green surface (Fig. 3A). Participants reached to the target and then acquired it by holding the blue cursor for 300 ms within 0.5 cm of the target's centre. Once the target was acquired, the cursor and target disappeared. Participants then returned their hand straight to the magnetic dock and proceeded to the next trial.

In the Rotated session of the experiment (Figure 1B), we had one group who trained with a 30° rotation (i.e. counter-clockwise) and the other trained with a 60° rotation (i.e. counter-clockwise) applied to the blue cursor. This meant that participants would have to counter the rotation by adjusting their reaches -30° or -60° (i.e. clockwise) to acquire the target. In the

Rotated sessions, the surface color of the table was navy blue to cue participants that these were the trials that some sort of compensation was required.

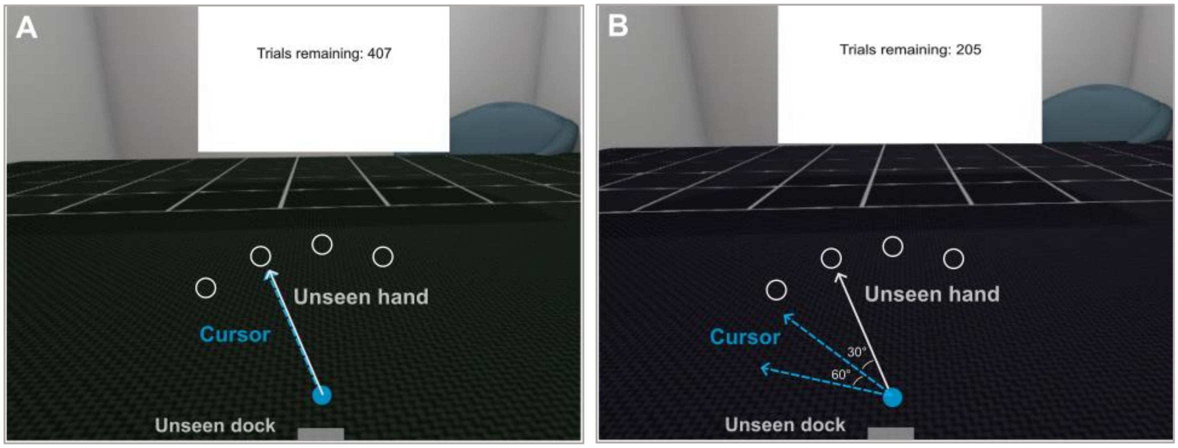


Figure 1: Hand Experimental stimuli. **A)** In 'Reach to Target' tasks in the 'Aligned' session, the blue cursor representing the hand followed the unseen hand path (**B)** In the 'Rotated' session of the experiment, a 30° or 60° CCW perturbation applied to the blue cursor so that participants had to reach 30° or 60° to the right to match the cursor path to the unseen hand path.

No Cursor. No Cursor trials measured reach aftereffects following visuomotor adaptation training. At the start of this block of trials, participants saw the words 'No Cursor' displayed on the screen. These trials were like the Reach to Target trials, but participants reached to targets in the absence of visual feedback provided by the blue cursor. The targets were the same four targets as the Reach-to-Target tasks and had a dark gray surface in both aligned and rotated sessions for participants to receive a visual cue when completing these trials, along with instructions from the experimenter. To get an idea of how far out they were required to reach, a blue arc, spanning 180° was centered on the home position and followed the outward movement of the unseen hand, similar to the illustration in Fig. 2A. Once they believed that they had acquired the target, they held their hand in place for 500 ms with minimal movement after moving at least 3cm out from home. The criterion for minimal movement was objectively defined and implemented by calculating the magnitude of movement as the distance between the home position and the controller position. Time was measured as the elapsed time between consecutive frames to examine the 500 ms hold. This triggered the end of the trial, making the target and arc disappear. Participants then returned their hand to the dock position and proceeded to the next trial. In the rotated session of the experiment, participants were instructed to not use any strategies they may have learned/used earlier and to treat these trials as the previous No Cursor trials during the first baseline session.

Localization. In the localization trials, participant estimated the location of their unseen hand. Participants held the right controller with their unseen right hand and were instructed to make volitional hand movements from the home position to self-directed points on a white arc (0.5 cm thick), located 12 cm away from the home position (as illustrated in Fig. 2A). To ensure a large range of unseen hand or pen locations, this arc spanned 60°, and the centre of the arc was varied across trials: 70°, 90°, 110° or 130° in polar coordinates. Similar to the No Cursor trials, a blue arc, spanning 180° moved with the participants outward unseen hand movement to indicate how far they had moved. Once the hand moved 12 cm from the home position and remained stationary for 500 ms while the blue arc overlapped with the white target arc, a 180° white arc appeared. The criterion for the hold was objectively defined and implemented by calculating the magnitude of movement as the distance between the home position and the controller position. Time was measured as the elapsed time between consecutive frames to examine the 500 ms hold. Participants then used their left controller’s joystick to move the red indicator along this arc to where they felt their unseen right thumb intersected the arc (as illustrated in Fig. 2B). They then indicated their final position by holding the trigger button on the left controller for a split second. After the arc and indicator disappear, they then returned their right hand to the dock and waited for the next trial to begin. This way, we were able to measure participants' estimates of the location of their unseen hand both before and after adapting to a rotated cursor.

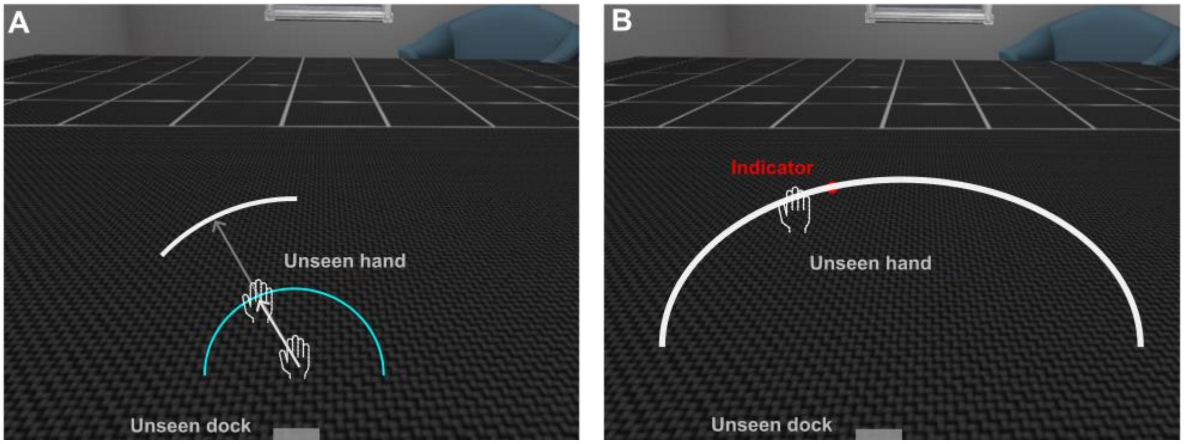
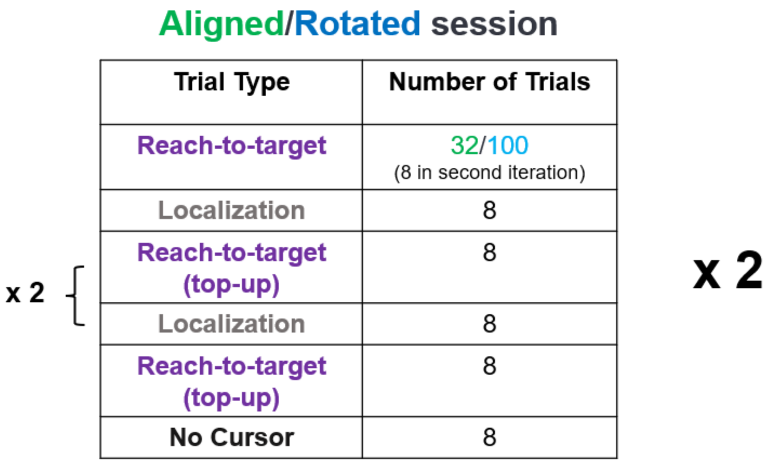


Figure 2: Localization trials. **A)** Participants reached out to anywhere along a white arc using their unseen right hand **(B)** Then, participants used their left controller's joystick to move the red indicator to where their right hand crossed the white arc. The blue arc expanded as the unseen hand moved outward for participants to know how far they need to reach out to acquire the arc.

Procedure

In the Hand Experiment, we aimed at replicating previous results on a robot manipulandum in the VR environment. Before starting the experiments, participants completed a practice round with 16 Reach-to-Target, 8 Localization, and 8 No Cursor trials to familiarize themselves with the movements they will be required to make in the experiment. Figure 3 illustrates the order of the trials for the Hand Experiment following these practice trials. The experiment began with the Aligned Reach-to-Target (iterations 1-2) where cursor reaches were made with the cursor movement-direction that was aligned with that of the unseen hand. The very first block of cursor-reaches consisted of 32 Aligned Reach-to-Target trials. These trials were followed by alternating between three blocks of top-up Reach-to-Target (8 trials/block) with three blocks of Localization trials (8 trials/block), ending each iteration off with one block of No Cursor reaches (8 trials/block). Each set of 8 trials (Aligned Reach to Target, No Cursor or Localization) repeated each of the four target or arc positions twice in a pseudo-randomized order. After each iteration, participants were given a short break of about 30 seconds to rest their hands. Once the aligned session (end of iteration 2) was complete, participants were given a mandatory break to rest their hands and arms before moving on to the Rotated session (blue in Fig.3) of the experiment. Participants continued wearing the headset and did not take it off at any point during the experiment.


Aligned/Rotated session

Trial Type	Number of Trials
Reach-to-target	32/100 (8 in second iteration)
Localization	8
Reach-to-target (top-up)	8
Localization	8
Reach-to-target (top-up)	8
No Cursor	8

Figure 3. Experiment Schedule for Hand Experiment. All participants followed the same sequence of tasks. Participants performed two iterations of the aligned session and took a mandatory short break before proceeding to the rotated session which also consisted of performing two iterations. The “Reach-to-Target” tasks in the Rotated session had either a 30° or 60° CCW visuomotor rotation.

After the mandatory break, participants completed the Rotated session where the cursor was perturbed 30° or 60° CCW for all Reach to Target trials (bottom row of Fig. 3). Participants were told that the cursor will move a bit differently, but were instructed to still try their best to acquire the target while continuing to make fast, straight and accurate reaches. The Rotated session consisted of the same number of iterations discussed in the Aligned session. The first rotated iteration (Reach to Target) was increased from 32 to 100 to allow participants to fully adapt to the misaligned cursor. This was followed by the same blocks of trials as completed in the Aligned session to measure changes in No-cursor reaches or estimate of hand location following adaptation. For the No Cursor trials, participants were instructed to exclude any strategy they developed to counter the visuomotor rotation so that any change, i.e. reach aftereffect, would be implicit. After the end of the fourth iteration, the rotated session was complete, at which point participants were instructed to remove the headset since they completed the approximately 50-minute-long experiment.

Pen Experiment

In this second experiment, the goal was to examine whether similar adaptation and shift in localization emerged when reaching was done with a pen. The procedure for the pen experiment was identical to the original experiment with the hand-cursor version, except they used the tip of the pen to acquire targets, as illustrated in Figure 4.

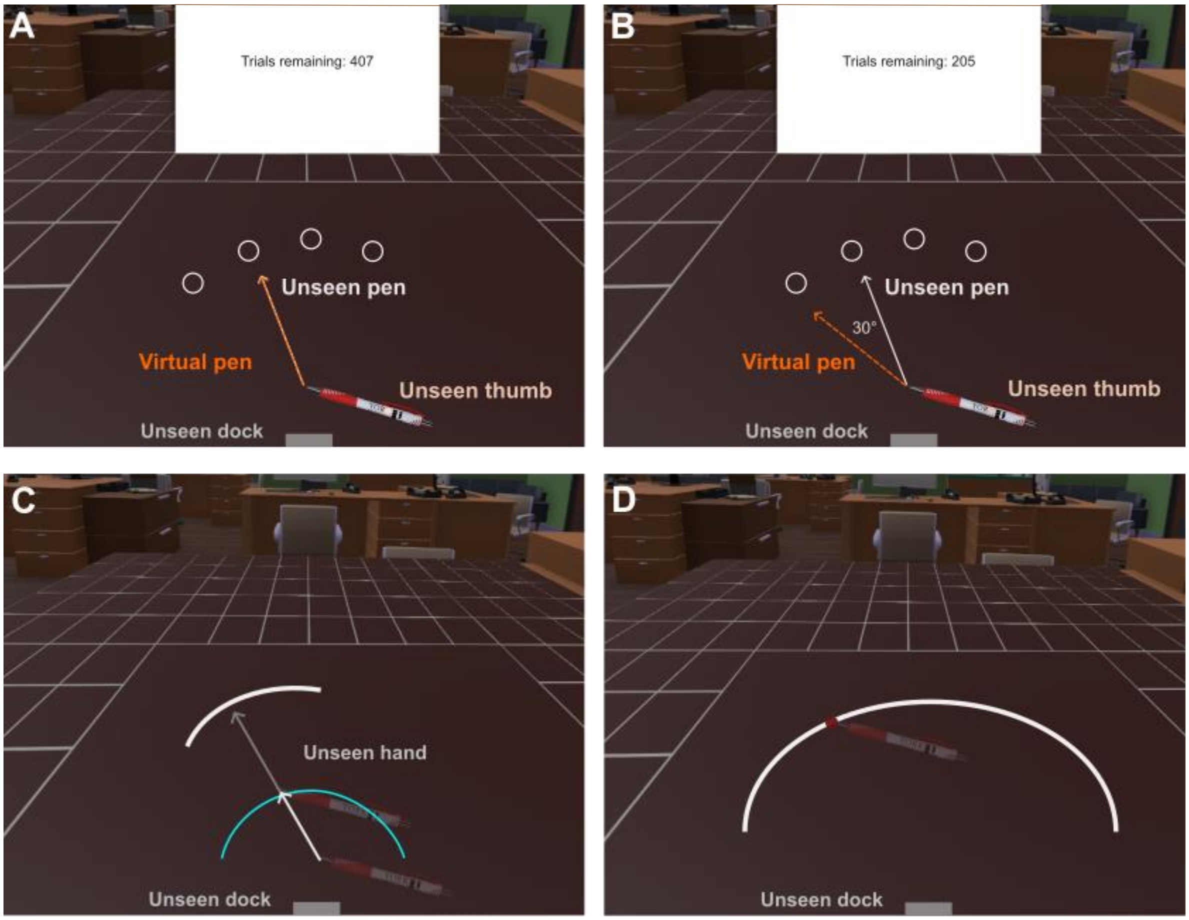
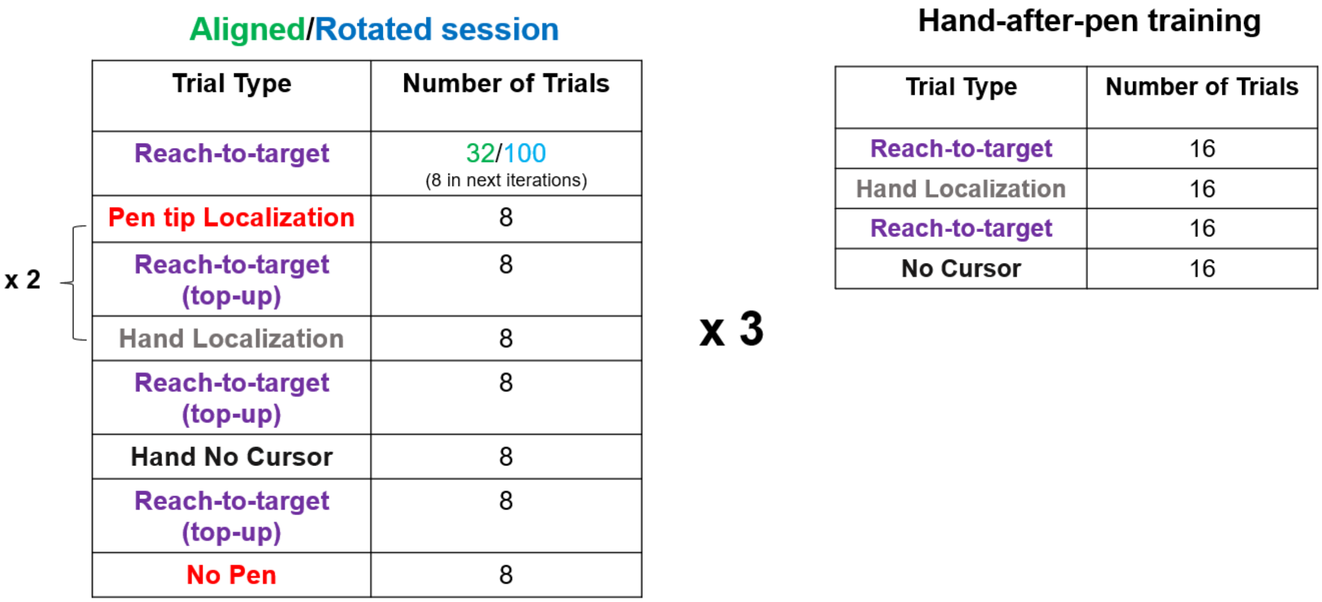


Figure 4: Pen Experimental Stimuli. **A)** In pen ‘Reach to Target’ tasks in the ‘Aligned’ session, the pen tip followed the unseen physical pen path (**B)** In the ‘Rotated’ session of the experiment, a 30° CCW perturbation was applied to the tip of the pen so that participants had to reach 30° to the right with the physical pen to match the virtual pen path to the physical pen path (**C)** In the pen localization task, participants reached out to anywhere along a white arc using the unseen tip of the pen **(D)** Then, participants used their left controller’s joystick to move the red indicator to where the unseen tip of the pen crossed the white arc. The blue arc expanded as the pen tip moved outward for participants to know how far they need to reach out to acquire the arc.

Procedure

The order of trials for the Pen experiment was very similar to the Hand Experiment with the addition of pen tip localization and no pen blocks, alongside the hand localization and no cursor blocks as illustrated in Figure 5. When switching from hand to pen and pen to hand trials, participants received a clear verbal cue to ensure that they were making accurate reaches.



Aligned/Rotated session

Trial Type	Number of Trials
Reach-to-target	32/100 (8 in next iterations)
Pen tip Localization	8
Reach-to-target (top-up)	8
Hand Localization	8
Reach-to-target (top-up)	8
Hand No Cursor	8
Reach-to-target (top-up)	8
No Pen	8

x 2

x 3

Hand-after-pen training

Trial Type	Number of Trials
Reach-to-target	16
Hand Localization	16
Reach-to-target	16
No Cursor	16

Figure 5. Experiment Schedule for Pen Experiment. All participants followed the same sequence of tasks. Participants performed two blocks of the aligned session and took a mandatory minimum 20-minute break before proceeding to the rotated session. The "Reach-to-Target" tasks in the Rotated session consisted of a 30° CCW visuomotor rotation. Participants then ended off the experiment with training the hand.

The Aligned session (iterations 1-3 in green) had four blocks of hand and tool localization which served as baseline data (shown in Fig. 5). They received short breaks after each iteration and a longer, minimum 20-minute mandatory break after the Aligned session (approximately 50 minutes long) was complete at which point they removed to the headset. They even had the option to return the next day, to avoid fatigue for this longer study.

In the Rotated session (iterations 3-6 in blue; Fig. 5), the movement of the tip of the virtual pen was perturbed 30°, relative to home position, for all Reach to Target trials. To counter this rotation, participants had to reach in a direction -30° relative to the target in addition to the translation of holding the pen. The Rotated session consisted of the same blocks and three iterations as discussed in the Aligned session. However, the number of trials in Reach to Target were increased to saturate learning of the visuomotor rotation. Similar to the Hand Experiment, during the No Cursor and No Pen tasks, participants were instructed to not use any strategy when reaching to the target. At the end of the Rotated session, participants completed the hand-after-pen task where they were instructed to acquire the following rotated reaches using their hand (hand-after-pen in Fig. 5), not the pen, followed by hand localization and no cursor trials. This was to show the effects of training the hand after training with a pen. Once this final task was over, the approximately 50-minute-long study was complete, and participants removed the headset.

Data analysis

All position measures were recorded using Unity 3D (2020.1.17, Unity Technologies, San Francisco, CA). All data preprocessing and analyses was conducted in R version 3.4.4 and data and analysis scripts can be found in this project's Open Science Framework repository (https://osf.io/vzds5/).

We aimed to determine if the shift in perceived location of an end-effector, following visuomotor rotation adaptation is also observed in VR environments and if it extends to tools as end effectors. Specifically, we will investigate any differences in performance for all trial types, across the five experimental groups, relative to baseline measures (aligned sessions).

To measure adaptation, outward reaches during the first 100 training trials of Reach-to-Target trials in the Rotated session were analyzed. Adaptation performance was quantified as the angular deviation between the cursor direction from home position and the angle of a straight line from home to target when the cursor was at 3 cm out from home to obtain the ballistic part of the movement before correction.

Our analysis consisted of five groups: hand-cursor 30° and hand-cursor 60° from the Hand Experiment and pen-tip 30°, hand-during-pen, hand-after-pen from the Pen Experiment.

For all measures, we calculate angles of points relative to the home position, e.g. the end point of reach with or without visual feedback or points indicated during any of the localization trials. Estimates of unseen hand and pen location were calculated by subtracting the angle of the endpoint of the unseen hand or pen, relative to the home position, from the angle of the point where participants indicated they perceived their hand or the pen tip, also relative to the home position. Since participants were free to move their unseen hand or pen tip, there was no guarantee that participants moved to specific angles. The difference between the responses in the aligned and rotated sessions represents the shift caused by training with rotated feedback on the perceived location of the hand or pen. For all statistical analyses, we used the medians of these values for each participant as medians are less sensitive to outliers. Since the cursor/pen tip was rotated 30° (i.e. CCW), localization shifts should also be in the CCW or positive direction.

The rate and extent of adaptation was tested by comparing the first two sets and then the last trial sets of 4 trials (one reach to each target) for the first 100 Reach-to-Target tasks of the rotated sessions (first Reach-to-Target task in Fig. 3 and in Fig. 5). The 3x4 mixed-effects ANOVA, with Greenhouse-Giesser corrections applied used degrees of error and included group (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-after-pen) as a between subjects factor. To determine if hand adaptation was faster after training with the pen, we performed a 2x2 ANOVA with only the first two trials from each group with group (hand-cursor 30°, hand-after-pen) as a within subject factor. The pen and hand-after-pen were completed by the same participants in the same session but since we wanted to test whether training with the pen facilitated adaptation to the hand-cursor, we included this as another level in the Group. We also investigated the effect of the magnitude of the rotation between hand-cursor 30° and hand-cursor 60° to see if participants adapted differently when training to a larger perturbation.

We removed outlier trials that fell ± 3 standard deviations from the mean in the no-cursor and no-pen trials. From the Hand Experiment, 0.88% of trials from the hand-cursor 30° group and 0.25% of trials from the hand-cursor 60° group were removed. From the Pen Experiment, 0.59% of trials were removed from the analysis. Median angular reach deviations were calculated for each participant by subtracting the endpoint angle (point where hand/pen tip intersects the arc) from the target angle. We tested for error deviations between the aligned and rotated sessions in the No-Cursor and No-Pen tasks by running paired t-tests between the aligned and rotated sessions for each group with Bonferroni corrections applied. We then took the difference between these rotated and aligned deviations to compute the aftereffects for each group. A one-way ANOVA of these aftereffects were run with group (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-during-pen, hand-after-pen) as between-subject factor to investigate if there were significant differences between conditions in reach aftereffects with Bonferroni corrections applied.

We removed outlier trials that fell ± 3 standard deviations from the mean in the hand localization and pen localization trials. From the Hand Experiment, 0.08% of trials from the hand-cursor 30° group and 0.38% of trials from the hand-cursor 60° group were removed. From the Pen Experiment, 0.39% of trials were removed from the analysis. We then analyzed shifts in end-effector localization found in the hand and pen localization tasks during adaptation. To confirm significance, paired t-tests were performed between the aligned and rotated sessions in each group with Bonferroni corrections applied. We conducted a one-way ANOVA on the shift in localization from aligned to rotated session (subtracted as above for reach aftereffects) with group (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-during-pen, hand-after-pen) as a between-subject factors to see if there were significant differences between conditions in localization shifts after training and applied Bonferroni corrections.

Lastly, we then explored if shifts in pen and hand localization were related to reach aftereffects by computing Pearson's correlations between participants' median deviations in the No Cursor and No Pen reaches from both the Hand and Pen experiments.

Results

Learning rate during adaptation

Before investigating how the addition of a tool during training changes implicit reach aftereffects and localization, we first confirmed that participants did indeed learn the perturbation by the end of the first 100 reach training trials (Fig. 6). During initial trials, the errors resembled the size of the perturbation. However, by the end of the training, participants were able to compensate for 75-80% of the visuomotor rotation. This is confirmed by a main effect across the three trials set ($F_{(1.83,\ 179.60)} = 92.50$, $p < .001$, $\eta^2 = 0.27$, in a 3 (first, second, and last trial set) x3 (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-during-pen) mixed-effects ANOVA. However, this learning across trials did not vary across the three groups (no 3x3 interaction: $F_{(3.67,\ 179.60)} = 2.37$, $p = .059$, $\eta^2 = 0.02$), suggesting that all three groups adapted to their perturbation in a similar manner. Nonetheless, because of the larger errors (more compensation due to larger rotation) in the hand-cursor 60°group (pink curve) compared to the other two groups (illustrated in Fig. 6), there was a main effect of group ($F_{(2, 98)} = 10.86$, $p < .001$, $\eta^2 = 0.12$). This main effect of group effect persisted for the two additional 2x3 ANOVAs comparing pen and hand for 30° rotation, and between the 30° and 60° rotation. This suggests that across training, errors were a bit smaller for the pen group (purple curve) compared to the hand-cursor 30° group (blue curve in middle panel) at least for the trial sets tested. Given there were no interactions between trial and group for either the 3x3 nor follow-up ANOVAs, the overall reduction of errors was similar across groups.

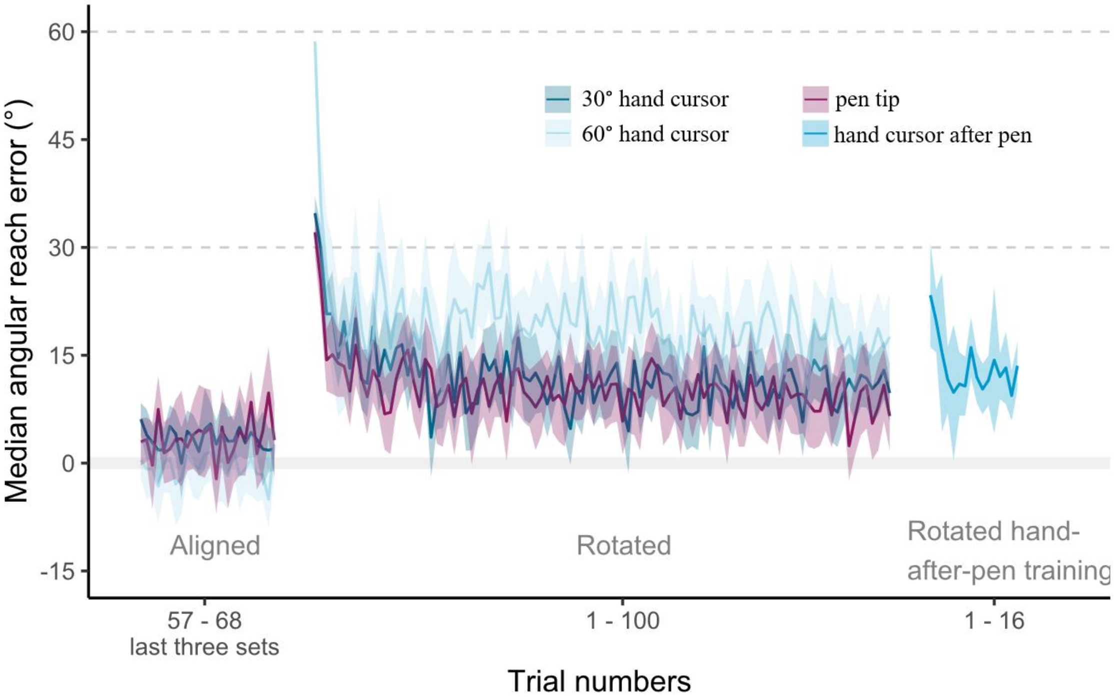


Figure 6. Learning during adaptation training. These plots represent the median angular reach deviation across all participants for each trial when participants reached to the target using their hand. The aligned phase depicts the last three sets (24 trials) of the aligned session (baseline data). The rotated phase consists of the first 100 trials of training in the rotated session. Hand after pen consists of the last chunk of Pen Experiment and had 32 trials where participants trained their hand after training with the pen. The grey solid line at the 0° mark indicates full compensate to the perturbation.

To determine whether people adapted faster in the hand-cursor 30° group following adaptation with a pen, we compared adaptation in the hand-after-pen group (rightmost blue curve) to the original hand-cursor 30° group (middle blue curve) for the first two trials (Fig. 6). To test for this generalization of learning from pen to hand, we performed a 2x2 ANOVA on the first two trials in the hand-cursor 30° and hand-after-pen groups. We only tested the first two trials, as we expected the generalization effect to be greatest at the start. Consistent with this, errors for the rotated hand-cursor after training with a rotated pen were smaller, indicating greater adaptation by the second trial ($t_{(122)} = 2.98$, $p = .018$) but not the first trial ($t_{(122)} = 2.21$, $p = .128$). Unsurprisingly, adapting to a perturbed pen did facilitate adaptation to the same perturbation applied to the hand cursor.

Reach aftereffects in hand and tool

We tested whether reach aftereffects emerged in the hand and pen experiments by analyzing reach trials without visual feedback (no-cursor, no-pen) before and after adaptation. Paired t-tests between the aligned and rotated types confirmed that aftereffects were produced for all groups as illustrated in Fig. 7A&B. In the Hand Experiment: aftereffects in hand-cursor 30° group ($t_{(24)} = 6.18$, $p < .001$) of 6.02° were observed (Fig. 7A left plot) and in the hand-cursor 60° group ($t_{(37)} = 9.73$, $p < .001$) aftereffects of 11.55° (Fig. 7A right plot). In the Pen Experiment, for the pen ($t_{(37)} = 8.72$, $p_{adj} < .001$) of 11.54° Fig. 7B left, hand during pen training ($t_{(37)} = 8.11$, $p_{adj} < .001$) of 8.93° shown in Fig. 7B middle, hand-after-pen ($t_{(37)} = 8.94$, $p_{adj} < .001$) of 10.67° (Fig. 7B right).

We compare the size of these aftereffects across groups in Fig. 7C by running a one-way ANOVA with group (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-during-pen, hand-after-pen) as between subject factors. We found a significant group effect ($F_{(4,172)} = 2.46$, p =

.047). Follow up tests revealed that the hand-after-pen training group had slightly larger aftereffects of 4.65° than the hand-cursor 30° group ($t_{(172)}$ = 2.54, p = .048). However, there was no significant change in reach aftereffects between the hand-cursor 30° and hand-cursor 60° groups ($t_{(172)}$ = 2.44, p = .064) nor hand-during-pen ($t_{(172)}$ = 1.04, p = 1.00). Reach aftereffects in the hand remained constant during the Pen Experiment and did not significantly differ during or after training with the pen ($t_{(172)}$ = 1.68, p = .380). Despite some differences being significant, they are only a few degrees larger and might not mean much in practice. Therefore, aftereffects emerged after training with a cursor and with a pen in a virtual environment.

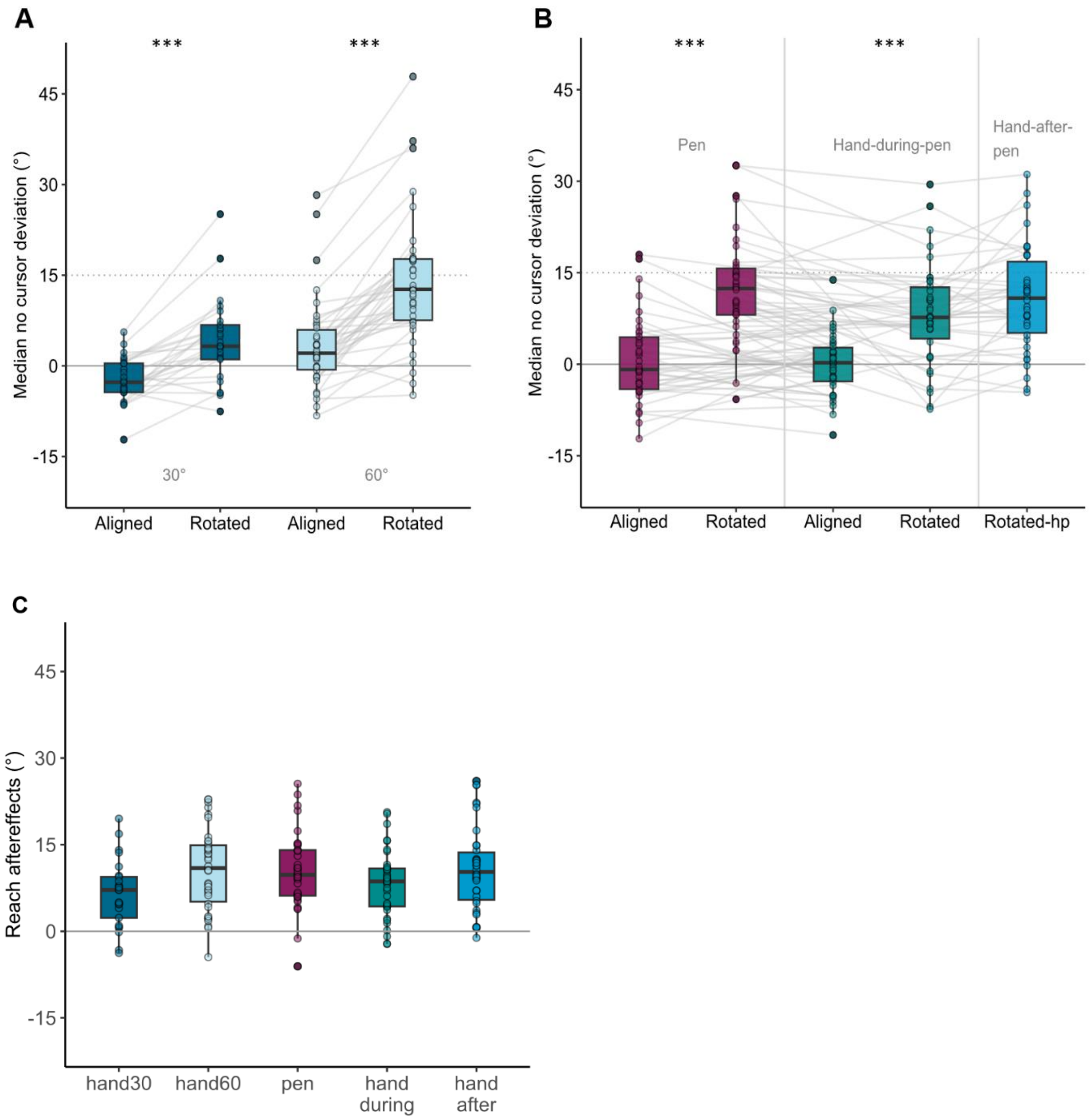


Figure 7. No-cursor/no-pen deviations and aftereffects. The boxes summarize the data distribution, providing information on the median, spread, and presence of outliers across trials. The data was inverted for easier comparison between the no-cursor and localization plots. Each data point represents a single participant's median reach deviation across all no-cursor/no-pen trials (A) In the Hand Experiment, median reach deviations were plotted against type (aligned and rotated) for each participant for the 30° (left) and 60° (right) groups. (B) shows the median reach deviations in the Pen Experiment for no-pen trials (left), for no-cursor trials during pen training (when participants moved their hand to the target; middle), and no-cursor reaches after subsequently training with the pen (right). (C) illustrates the reach aftereffects across the different groups.

Shifts in end effector localization

We then moved on to investigate our main question, if shifts in end effector localization emerged during the different sessions. Specifically, for hand after training in the Hand Experiment, pen and hand-during-pen, and hand-after-pen training in the Pen Experiment. All groups appeared to show shifts in localization, except for the hand-cursor 30° group (as shown in Fig. 8): Specifically, paired t-tests indicated a significant shift in estimate of hand for hand-cursor 60° group (($t_{(37)} = 8.31$, $p < .001$) of 10.62°, but surprisingly not for hand-cursor 30° group (($t_{(24)} = 1.62$, $p = .118$). Shifts were found to be significant for all groups in the Pen experiment: pen ($t_{(37)} = 5.31$, $p_{adj} < .001$) of 6.12°, hand-during-pen training ($t_{(37)} = 2.95$, $p_{adj} = .020$) of 2.26°, and hand-after-pen training ($t_{(37)} = 3.27$, $p_{adj} = .011$) of 3.57°. Shifts were slightly higher hand-after-pen training but did not significantly differ from hand-during-pen training. Nonetheless, as consistent with past studies, these shifts in localizations are consistently smaller than aftereffects. That we found a significant shift for the 30° rotation for hand-cursor both during and after training with the pen but not when just training with the hand-cursor was not expected. The hand-cursor 30° groups had a rather large positive bias in our baseline condition which may have masked what is usually small shift in localizing the unseen hand.

We conducted a one-way ANOVA with group (hand-cursor 30°, hand-cursor 60°, pen-tip 30°, hand-during-pen, hand-after-pen) as within subject factors and found a significant group effect ($F_{(4,172)} = 9.71$, $p < .001$). Shifts were larger in hand-cursor 60° when compared to hand-cursor 30° ($t_{(172)} = 5.28$, $p_{adj} = .004$). There was no significant shift between hand-cursor 30° and hand-during-pen training ($t_{(172)} = 1.18$, $p_{adj} < .965$) and hand-after-pen training ($t_{(172)} = 2.39$, $p_{adj} = .072$). Furthermore, shifts in hand during and after the Pen Experiment did not significantly ary ($t_{(172)} = 1.36$, $p_{adj} = .700$). Therefore, training with a pen leads to significant shifts in hand localization even when hand-cursor was not trained and similar shifts were observed in all groups, except for hand-cursor 30° group (Fig. 8C).

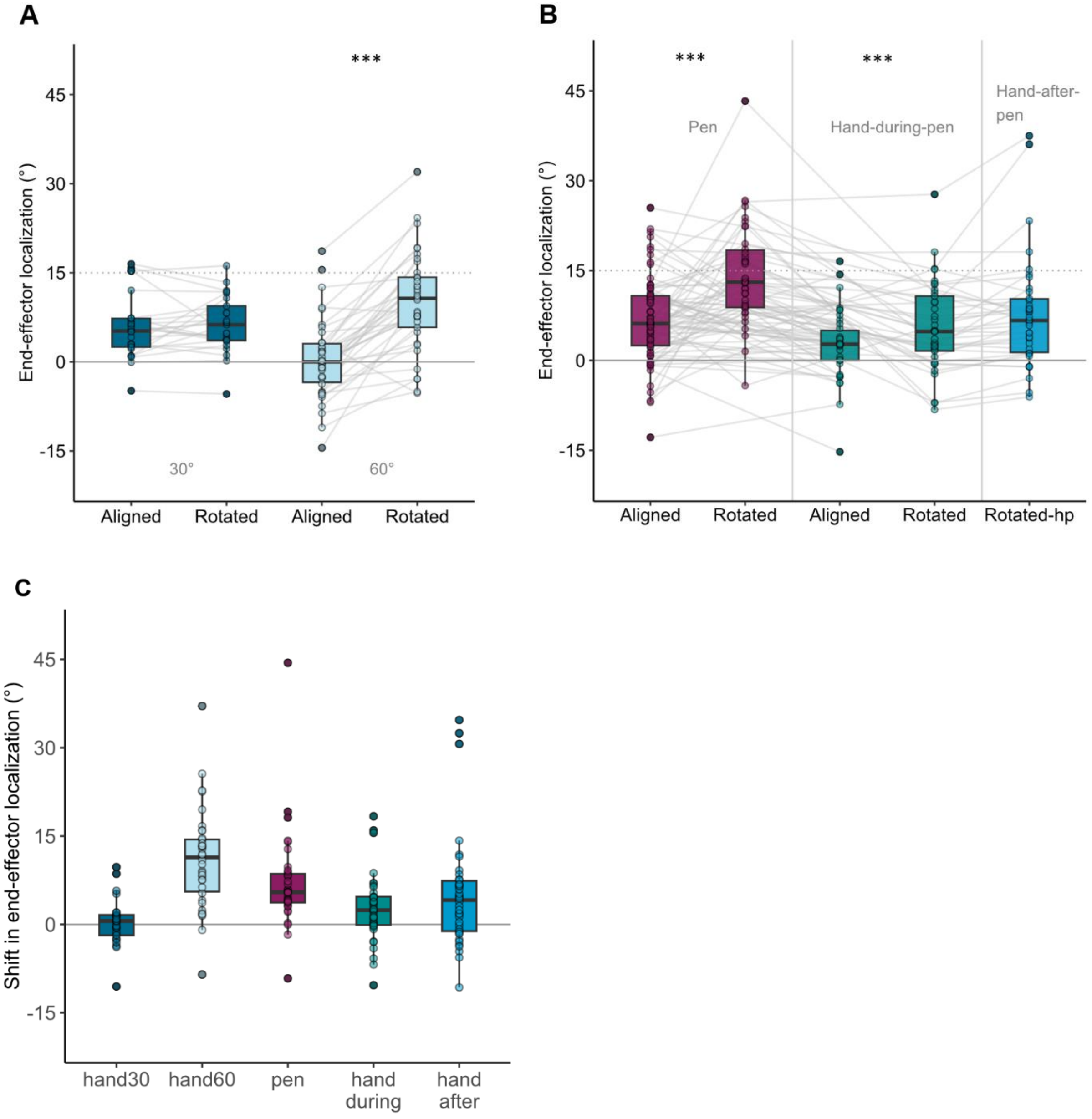


Figure 8. End-effector localization and shifts. The boxes summarize the data distribution, providing information on the median, spread, and presence of outliers across trials. Each data point represents a single participant's median localization errors relative to the actual position of the hand or pen in degrees angle, across all no-cursor/no-pen trials. (A) In the Hand Experiment, median hand end-effector deviations were plotted against type (aligned and rotated) for each participant for the 30° (left) and 60° (right)

groups. (B) shows the median end-effector localization error in the Pen Experiment for pen (left), hand during pen training (middle), and hand after training with the pen (right). (C) illustrates the shifts in end-effector localization in each condition.

Lastly, we then explored shifts in pen and hand localization were related to reach aftereffects (Fig. 9). We found that the linear regression model that includes both the main effects of aftereffects and shift as well as their interaction with the group variable was significant ($F_{(9,167)} = 10.45$, $p < .001$, $r^2 = 0.326$, slope = 0.36). That is, larger reach aftereffects were associated with larger shifts. And while the slopes were all positive for all groups, the relationship for most of the groups was weak with r^2 of 0.08 to 0.16, except for the hand-cursor 60° group ($\beta = 0.44$, $r^2 = 0.463$, $p = .085$). Nevertheless, if both reach aftereffects and localization shifts rely on implicit adaptation processes, it makes sense that they are somewhat related

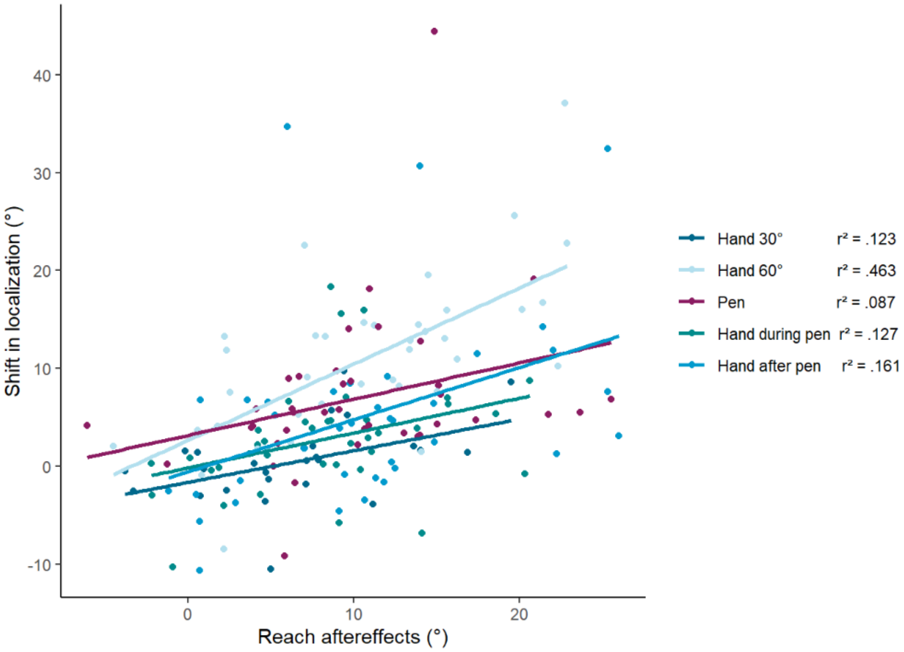


Figure 9. Relationships between changes in hand and pen localization, reach aftereffects for no cursor and no pen reaches across both the Pen and Hand Experiments. The y-axis shows the mean shift in localization for each participant and the x-axis represents each reach aftereffects for both hand and pen for each participant. The solid lines correspond to a regression line and individual data points are color coded according to the corresponding groups.

Discussion

The goal of this study was to investigate whether adapting to reaching movements made with a tool, i.e. a pen, in immersive VR affects the perceived location of the unseen tool and hand. We also compared these changes in movements and perceived location of the pen to those made with a more conventional hand-cursor. In the Hand Experiment, participants reached out to targets using a hand-cursor whose motion was rotated either by 30° or 60° relative to the unseen hand. We found that learning rate was comparable, but reach aftereffects were larger for those who trained with the larger 60° perturbation. Only the group adapting to the 60° visuomotor rotation showed the typical shift in perceived location of the unseen hand. In the Pen Experiment, participants reached to the same targets using the tip of the pen whose movement direction was also misaligned by 30°. We found that rate and extent of adaptation, and resulting reach aftereffects were comparable or marginally better when using the pen compared to the hand-cursor in the Hand Experiment. Moreover, adaptation training with the pen led to comparable, pen aftereffects and perceived shifts in location of both the unseen pen and the unseen hand within this same experiment. Interestingly, although we did not observe shifts in the perceived location of the unseen hand in the Hand Experiment with the 30° rotation, we did find these shifts both during adaptation with the pen and after brief training with the hand-cursor following adaptation with the pen. Thus, for the most part, the perceptual changes in the end-effector location that typically occur during hand-movement adaptation to visual perturbations in two-dimensional space also extend to hand-held tools and three-dimensional environments.

To optimally interact with our environment, we are required to continuously readjust our movements, especially when adjusting to a different tool (Krakauer et al., 2019). While previous studies have measured reach adaptation using the conventional hand-cursor, this is the first study to explore reach adaptation with a tool in immersive VR. By the end of training with a pen, participants compensated for the rotations by 75-80% which is comparable to other studies that use classic visuomotor rotation training (Gastrock et al., 2020; Modchalingam et al., 2019; Krakauer et al., 2019; Block & Lui, 2023). Here, we not only show that participants were able to adapt to the perturbation when using a pen, but this led to slightly faster learning when reaching to rotated hand-cursor in the "hand after pen" training session. While the errors in the first reach were similar to those made by naïve participants (who didn't train with the pen), the error on average were smaller (indicating greater compensation) by the second reach in hand-after-pen (those who first trained with the pen). Note despite the same rotation and same targets, just switching from pen to hand-cursor led to an initial increase in error and compared to where the pen left off at the end of pen-training (right side of the Figure 6). This incomplete transfer of adaptation in the initial hand-reaches follow pen adaptation (hand after pen) suggests that pen-mediated and direct hand movements are treated by the motor system as different end-effectors, despite identical targets and perturbations. This indicates that adapting movements made with a pen does not fully prepare the motor system for subsequent hand-only cursor control. The change in the physical interface (pen to no pen) appears to be substantial enough to impact performance, even when other task parameters remain constant. How learning generalizes can provide some insight into the shared neural representations underlying learning (Krakauer et al., 2019). A possible explanation for the faster adaptation of the hand when following the pen could be due greater sensitivity to errors or an unconscious or conscious knowledge of visuomotor mapping needed to compensate for the perturbation across end-effectors. However, the similar magnitude of aftereffects observed after training with both the hand and pen in the virtual environment suggests that a portion of this adaptation is unconscious or implicit. This shift in estimate of the unseen hand location during pen training may have contributed to the faster adaptation of the hand-after-pen training sessions. All hand groups before and after training with the pen were comparable and showed similar size aftereffects typically observed with a hand-cursor (Modchalingam et al., 2019; Gastrock, et al., 2020; Salomonczyk et al., 2011; Clayton et al., 2014; Tsay et al., 2022; Crevecouer et al., 2020), suggesting that the brain recalibrates the estimated position of unseen hand even when it is merely holding the tool that is being wielded.

While many studies have shown that training to reach to targets with a misaligned cursor, or in a force curl-field, is sufficient to lead to a robust change in estimate of hand positions (‘t Hart & Henriques, 2016; Gastrock, et al., 2020; Modchalingam et al., 2019; Ruttle et al., 2018; Salomonczyk et al., 2011; Zbib et al., 2016; Izawa et al., 2012; Rand & Heur, 2019; Ostry et al., 2010; Ohashi et al., 2019), this study is the first to show that changes in estimate of unseen location of end-effectors applies to tools. Except for the 30° hand-cursor group, all other hand groups during and after pen training showed similar shifts in end-effector localization, as typically observed in hand-cursor localization (‘t Hart & Henriques, 2016; Gastrock, et al., 2020; Modchalingam et al., 2019; Ruttle et al., 2018; Salomonczyk et al., 2011; Zbib et al., 2016; Izawa et al., 2012; Rand & Heur, 2019). We were surprised not to find a significant shift in the 30° hand-cursor group which would be attributed to the large positive bias found in baseline, making the shift less detectable (Fig. 9). Reach aftereffects and shifts in end-effector localization are consistent with the idea that adaptation partly involves updating internal models of both the hand and the pen. Further research is necessary to investigate whether these shifts also reflect tool embodiment. Research has shown that extensive tool use enables the body to perceive the tool as an extension of one’s own body and impacts behavioural, perceptual, and physiological responses to the environment (Weser & Proffitt, 2021). Tool-use causes the brain and sensory systems to adapt, integrating the tool into the body’s schema (Bell et al., 2021; Weser & Proffitt, 2021). On the other hand, Schone et al. (2021) finds that expert tool users represent the tool less like a hand and have more distinct tool representation throughout the visuomotor network, categorizing the tool. For experts to optimally wield a tool, the network differentiates the hand and tool representations to minimize interference and effectively store and access information so they can better switch between using the tool or the hand (Schone et al., 2021). In the current study, given that we found shifts in both pen and hand localization (Pen Experiment), participants are aware of the pen being added on to the hand and that both hand and pen are separate entities. Therefore, we can update our internal model to include a tool when used extensively. However, further research is required to truly understand the neural networks involved during tool use to differentiate between tool embodiment and categorization. It is important to note visuomotor studies typically use a digitizing tablet or VR that already have participants grasp onto a controller or pen. This represents their hand which can be considered as a “tool” attached to participants’ hands. Therefore, future research could focus on using different equipment such as Opti track or newer models of VR headsets that do not require the use of controllers to track hand movements.

Lastly, unlike previous studies, we found that the size of cursor-rotation did influence both the size of the reach aftereffect and shift in localization. Previous research has shown that regardless of perturbation size, comparable reach aftereffects and shifts emerge (Modchalingam et al., 2019; Salomonczyk et al., 2011). We find larger reach aftereffects and shifts in the 60° hand-cursor group than the 30° hand-cursor group. However, the shifts and reach aftereffects that emerge in the 60° hand-cursor group are comparable to those observed in 30° hand during pen training and 30° hand after pen training. It is possible that in VR, people expect some form of anomaly and unconsciously consider the feedback in VR less reliable which in turn decreases aftereffects and shifts in localization. Whatever happens is not indicative of something real, so they reduce their proprioceptive recalibration.

VR is being increasingly used for rehabilitation and since it is easily accessible, understanding its effectiveness in the clinical population is important. VR environments reduce the risk of visual recalibration by giving the experimenter the ability to only shift the location of the seen hand rather than shifting the entire workspace (Henriques & Cressman, 2012). Understanding motor adaptation could help individuals with neurological disorders that cause sensorimotor malfunction in rehabilitation (Henriques & Cressman, 2012). Although the cerebellum plays an important role in motor adaptation, patients with mild cerebellar ataxia are able to experience proprioceptive recalibration when training to a gradually introduced perturbation (Mostafa et al., 2019; Izawa et al., 2012; Modchalingam et al., 2023). Taken together, we find that training with a pen results in reach aftereffects and shifts in end-effector localization and that pen training significantly changes estimate of hand location or hand-only reach aftereffects.

Conclusion

In this study, we found that in immersive VR, adapting to pen reaches leads to significant changes in reach aftereffects and estimates of pen and hand location. Future studies should focus on making the study more ecological where participants maneuver the tool as they would in real life and train with the tool. This research provides further insight for use in VR based rehabilitation programs. Understanding how we interact with tools in a virtual environment can help develop more targeted and effective rehabilitation interventions. By manipulating virtual environments and incorporating specific tools, therapists could create more engaging interventions targeted towards patients' needs and goals.

References

Alzayat, A., Hancock, M., & Nacenta, M. A. (2019, May). Quantitative measurement of tool embodiment for virtual reality input alternatives. In *Proceedings of the 2019 CHI Conference on Human Factors in Computing Systems* (pp. 1-11).

Anglin, J. M., Sugiyama, T., & Liew, S. L. (2017). Visuomotor adaptation in head-mounted virtual reality versus conventional training. *Scientific reports*, *7*(1), 45469.

Barkley, V., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2014). Reach adaptation and proprioceptive recalibration following terminal visual feedback of the hand. *Frontiers in Human Neuroscience*, *8*, 705.

Bell, J. D., & Macuga, K. L. (2022). Are tools truly incorporated as an extension of the body representation? Assessing the evidence for tool embodiment. *Psychonomic Bulletin & Review*, *29*(2), 343-368.

Block, H. J., & Liu, Y. (2023). Visuo-proprioceptive recalibration and the sensorimotor map. *Journal of Neurophysiology*, *129*(5), 1249-1258.

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of neurophysiology*, *113*(10), 3836-3849.

Borrego, A., Latorre, J., Alcañiz, M., & Llorens, R. (2018). Comparison of Oculus Rift and HTC Vive: feasibility for virtual reality-based exploration, navigation, exergaming, and rehabilitation. *Games for health journal*, *7*(3), 151-156.

Brookes, J., Warburton, M., Alghadier, M., Mon-Williams, M., & Mushtaq, F. (2020). Studying human behavior with virtual reality: The Unity Experiment Framework. *Behavior research methods*, *52*, 455-463.

Carter, A. R., Foreman, M. H., Martin, C., Fitterer, S., Pioppo, A., Connor, L. T., & Engsberg, J. (2016). Inducing visuomotor adaptation using virtual reality gaming with a virtual shift as a treatment for unilateral spatial neglect. *Journal of Intellectual Disability-Diagnosis and Treatment*, *4*(3), 170-184.

Clayton, H. A., Cressman, E. K., & Henriques, D. Y. (2014). The effect of visuomotor adaptation on proprioceptive localization: the contributions of perceptual and motor changes. *Experimental brain research*, *232*, 2073-2086.

Cressman, E. K., & Henriques, D. Y. (2010). Reach adaptation and proprioceptive recalibration following exposure to misaligned sensory input. *Journal of neurophysiology*, *103*(4), 1888-1895.

Crevecoeur, F., Thonnard, J. L., & Lefevre, P. (2020). A very fast time scale of human motor adaptation: within movement adjustments of internal representations during reaching. *eneuro*, *7*(1).

Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behavioural brain research*, *219*(1), 8-14.

Gastrock, R. Q., Modchalingam, S., ’t Hart, B. M., & Henriques, D. Y. (2020). External error attribution dampens efferent-based predictions but not proprioceptive changes in hand localization. *Scientific Reports*, *10*(1), 19918.

Gastrock, R. Q., ’t Hart, B. M., & Henriques, D. Y. (2024). Distinct learning, retention, and generalization patterns in de novo learning versus motor adaptation. *Scientific Reports*, *14*(1), 8906.

Henriques, D. Y., & Cressman, E. K. (2012). Visuomotor adaptation and proprioceptive recalibration. *Journal of motor behavior*, *44*(6), 435-444.

Izawa, J., Criscimagna-Hemminger, S. E., & Shadmehr, R. (2012). Cerebellar contributions to reach adaptation and learning sensory consequences of action. *Journal of Neuroscience*, *32*(12), 4230-4239.

Jones, S. A., Cressman, E. K., & Henriques, D. Y. (2010). Proprioceptive localization of the left and right hands. *Experimental brain research*, *204*, 373-383.

Juliano, J. M., Schweighofer, N., & Liew, S. L. (2022). Increased cognitive load in immersive virtual reality during visuomotor adaptation is associated with decreased long-term retention and context transfer. *Journal of NeuroEngineering and Rehabilitation*, *19*(1), 106.

Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor learning. *Compr Physiol*, *9*(2), 613-663.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in cognitive sciences*, *8*(2), 79-86.

Modchalingam, S., Vachon, C. M., ‘t Hart, B. M., & Henriques, D. Y. (2019). The effects of awareness of the perturbation during motor adaptation on hand localization. *PLoS One*, *14*(8), e0220884.

Modchalingam, S., Ciccone, M., D’Amario, S., ’t Hart, B. M., & Henriques, D. Y. (2023). Adapting to visuomotor rotations in stepped increments increases implicit motor learning. *Scientific Reports*, *13*(1), 5022.

Mostafa, A. A., ‘t Hart, B. M., & Henriques, D. Y. (2019). Motor learning without moving: proprioceptive and predictive hand localization after passive visuoproprioceptive discrepancy training. *PLoS One*, *14*(8), e0221861.

Ohashi, H., Valle-Mena, R., Gribble, P. L., & Ostry, D. J. (2019). Movements following force-field adaptation are aligned with altered sense of limb position. *Experimental Brain Research*, *237*, 1303-1313.

Ong, N. T., & Hodges, N. J. (2010). Absence of after-effects for observers after watching a visuomotor adaptation. *Experimental Brain Research*, *205*, 325-334.

Ostry, D. J., Darainy, M., Mattar, A. A., Wong, J., & Gribble, P. L. (2010). Somatosensory plasticity and motor learning. *Journal of Neuroscience*, *30*(15), 5384-5393.

Rand, M. K., & Heuer, H. (2019). Visual and proprioceptive recalibrations after exposure to a visuomotor rotation. *European Journal of Neuroscience*, *50*(8), 3296-3310.

Ruttle, J. E., 't Hart, B. M., & Henriques, D. Y. (2018). The fast contribution of visual-proprioceptive discrepancy to reach aftereffects and proprioceptive recalibration. *PLoS One*, *13*(7), e0200621.

Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2011). Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. *Neuropsychologia*, *49*(11), 3053-3062.

Schone, H. R., Maimon-Mor, R. O., Baker, C. I., & Makin, T. R. (2021). Expert tool users show increased differentiation between visual representations of hands and tools. *Journal of Neuroscience*, *41*(13), 2980-2989.

Shum, L. C., Valdés, B. A., & Van der Loos, H. M. (2019). Determining the accuracy of oculus touch controllers for motor rehabilitation applications using quantifiable upper limb kinematics: Validation study. JMIR Biomedical Engineering, 4(1), e12291.

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*, e76639.

‘t Hart, B. M., & Henriques, D. Y. (2016). Separating predicted and perceived sensory consequences of motor learning. *PLoS One*, *11*(9), e0163556.

Weser, V. U., & Proffitt, D. R. (2021). Expertise in tool use promotes tool embodiment. *Topics in cognitive science*, *13*(4), 597-609.

Zbib, B., Henriques, D. Y., & Cressman, E. K. (2016). Proprioceptive recalibration arises slowly compared to reach adaptation. *Experimental Brain Research*, *234*, 2201-2213.