Using Tools as Cues for Motor Adaptation in Virtual Reality

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Abstract

Humans are highly skilled at switching between tools, even when they demand opposing motor actions. This thesis investigates how people acquire and maintain distinct tool-specific motor memories by examining the cues that enable dual adaptation to conflicting sensorimotor demands. Using a visuomotor adaptation paradigm in immersive virtual reality (VR), we tested whether visual or movement-related tool features support separate internal models for opposing perturbations. Participants performed a shooting task with altered visual feedback, where each tool was associated with an opposing visuomotor rotation. Across three groups, tools differed only in colour (Colour Control), in shape but not movement direction (Motor Congruent), or both (Motor Incongruent). A single adaptation control group was also included. Only the Motor Incongruent group demonstrated robust dual adaptation and aftereffects, comparable to single tool learning. These findings suggest movement-specific features play a critical role in the formation of distinct internal models during tool learning.

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Glossary

Motor Learning: The process of acquiring, refining, and retaining motor skills through practice and experience, resulting in relatively permanent changes in movement capabilities.

Motor Adaptation: The error driven form of motor learning in which motor responses are gradually adjusted to compensate for changes in the body or environment.

Visuomotor Mapping: The relationship between visual input (e.g., target or cursor position) and motor output (e.g., hand or tool movement). Changes in this mapping, such as visuomotor rotations or distortions, require adaptation to realign visual and motor coordinates.

Internal forward model: A neural mechanism that predicts the sensory consequences of motor commands, usually based on efferent copy signals.

Efference copy: Internal copy of a motor command sent to the forward model, enabling the prediction of expected sensory feedback.

Motor Memory: The stored representation of previously learned motor commands and their outcomes, allowing past experience to shape future movement. Motor memory interacts with forward models to refine predictions and support long-term retention of adapted behaviors.

Control Policy: The task-specific rule or mapping that generates motor commands based on sensory input and goals. It specifies how movements should be executed to achieve desired outcomes.

Sensory prediction error: The difference between the observed error and predicted outcome (from the forward model) of a given movement, which serves as the primary teaching signal for motor adaptation.

Extrinsic cues: Contextual signals external to the movement itself, often visual in nature (background colour or object shape), that can modulate or trigger separate motor memories.

Intrinsic cues: Contextual signals inherent to the movement or body state (e.g., limb posture, movement direction, or effector used), which can serve as internal markers for motor learning and memory retrieval.

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General introduction

Tool use is a hallmark of human cognition, enabling humans to extend their capabilities beyond innate bodily functions. From ancient hand tools to modern digital interfaces, we skillfully learn and operate a wide range of tools to achieve task goals. This flexibility includes the remarkable ability to switch between tools that require distinct motor actions—for example, toggling between a knife and fork or alternating between a keyboard and mouse. Such adaptability reflects the brain's capacity to learn and retrieve multiple tool-specific motor plans without interference. However, the mechanisms by which the motor system acquires, stores, and distinguishes these tool-specific skills—especially when learned in parallel—remain poorly understood.

Neuroscientific evidence suggests that tools are neurally represented as separate effectors than the rest of the body. Functional neuroimaging studies show differential activation in motor-related regions when individuals act with their hands rather than tools (Gallivan et al., 2013). Tool-specific neuronal activation is so poignant that even miming tool use engages circuits specific to the actual tool movement (Johnson-Frey, 2004; Van Elk et al., 2011). This neural embodiment allows tools to be integrated into existing sensorimotor representations and supports the development of internal models that predict and adjust for the consequences of tool-based actions.

These internal models rely on forward predictions generated by the brain about the sensory outcomes of a movement. When a motor command is issued, an efference copy of the command is sent to a forward model that estimates the expected sensory feedback (e.g., where the tool or hand should go). This estimate is compared to the actual feedback received through vision or proprioception (Duhamel, Colby, & Goldberg, 1992; Colby & Duhamel, 1996;). The resulting sensory prediction error—the mismatch between predicted and observed feedback—is used to refine the internal model and improve future movements (Wolpert & Kawato, 1998; Tsay et al., 2022).

This process of motor adaptation depends on an internal computation often referred to as the control policy—the mapping from sensory input to motor output that governs how the brain generates appropriate motor commands for a given context. As shown in Figure 1, the control policy works in tandem with forward prediction to ensure accurate movement execution. In effect, the control policy selects and shapes motor commands based on task context, expected outcomes, and previous learning. When multiple tasks or tools are involved, dual adaptation requires the formation and retrieval of separate control policies, each appropriately linked to its associated context.

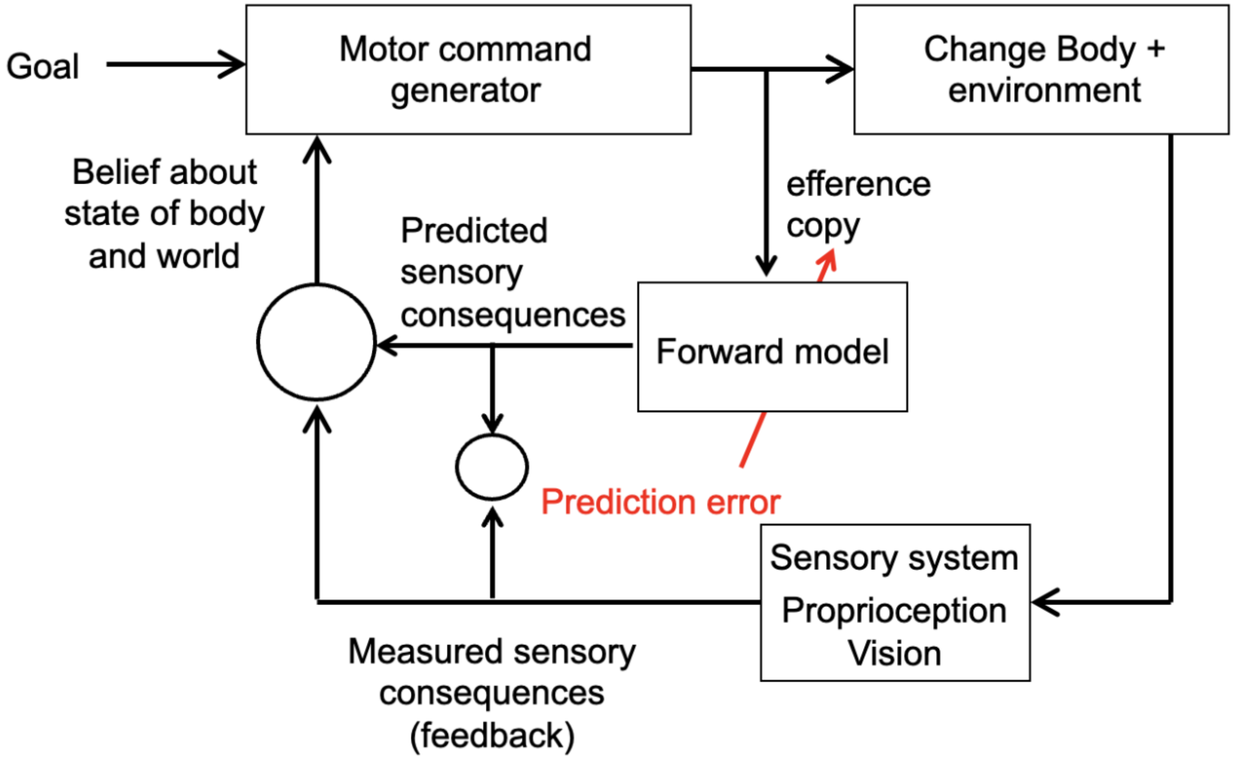

Figure 1. Sensorimotor control system underlying adaptation. Upon selecting a movement goal, the brain generates a motor command using a context-specific control policy. An efference copy of this command is sent to the forward model, which predicts the expected sensory outcome. The actual sensory feedback is then compared to this prediction to compute a sensory prediction error (small circle) which is used to update the forward model—refining future predictions (as indicated in red). The estimates provided by the updated forward model is combined with sensory feedback to estimate the current state of the body and environment (larger circle), and this refined state estimate is what informs adjustments to the control policy—altering how future motor commands are selected to better achieve the intended outcome. Together, this cycle supports accurate and adaptive movement control.

Early research on motor adaptation frequently employed the prism adaptation paradigm, where prism goggles were used to induce lateral or vertical shifts to the visual fields (e.g., Redding, Rossetti, & Wallace, 2005). More recently, visuomotor rotation tasks have become the dominant approach. In these tasks, participants make goal-directed reaches while receiving visual feedback. On “aligned” trials, the cursor accurately reflects hand direction. In other words, the cursor moves in the same direction as the unseen hand. To induce adaptation, a visuomotor rotation is applied: the cursor deviates from the hand path by a fixed angle (e.g., 30°), resulting in a mismatch between intended and observed cursor movement. Over these repeated “rotated” trials, participants learn to adjust their movement to compensate for the rotation, gradually reducing the error between the cursor and the target. This reduction in error across trials reflects motor adaptation. When the rotation is removed, aftereffects—persistent movement deviations—reveal the recalibration of the internal model, often occurring outside of conscious awareness and reflecting implicit learning.

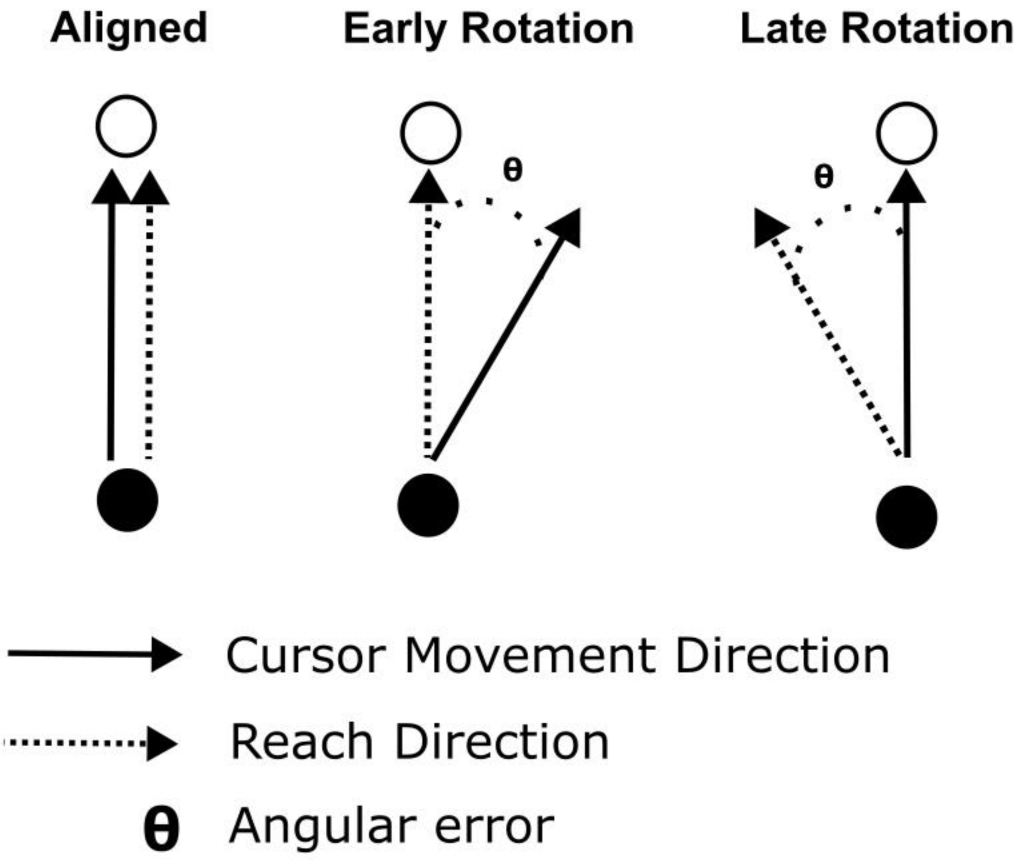

Figure 2. Visuomotor adaptation paradigm. Left: In aligned trials, the cursor and hand move in the same direction. Middle: When a visuomotor rotation is introduced (θ), the cursor deviates from the hand path. Right: Over time, participants adapt by aiming opposite the rotation so that the rotated cursor reaches the target.

Recently, these paradigms have been extended into immersive virtual reality (VR), where head-mounted displays simulate rich, interactive environments (Anglin, Sugiyama, & Liew, 2017; Verhulst, Namikawa, & Kasahara, 2022). VR provides a more ecologically valid platform for studying real-world tool use while allowing tight control over visual and motor dynamics. Though learning in VR can be slower—possibly due to increased cognitive demands—it offers the unique ability to dissociate visual features (e.g., tool shape) from motor dynamics (e.g., how the tool is used).

Dual Adaptation and the Role of Contextual Cues

While the visuomotor adaptation paradigm typically involves learning to compensate for a single perturbation, dual adaptation presents a more complex challenge: learning two opposing sensorimotor mappings (e.g., clockwise and counterclockwise cursor rotations) within the same experimental session. In the absence of contextual cues, compensation for opposing perturbations is often incomplete or unstable, as the motor system struggles to develop and maintain separate representations. This becomes particularly difficult when the perturbations are randomly interleaved, since learning one mapping typically interferes with the other. To resolve this interference, the motor system must be able to associate each perturbation with a distinct context and retrieve the appropriate internal model and control policy on a trial-by-trial basis.

A growing body of research has examined which types of contextual cues enable the formation of separate internal models given the specific control policy. A key distinction has emerged between intrinsic cues, which are those directly tied to movement execution, and extrinsic cues, which are visual or environmental features not involved in generating the movement itself. Intrinsic cues, such as starting posture (Ayala, 't Hart, & Henriques, 2015), movement direction (Hamel et al., 2022), muscle activation (Lee & Schweighofer, 2009), or lead-in motions (Forano & Howard, 2020), reliably support dual adaptation. These cues likely work because they engage different motor plans or control policies, allowing the system to encode separate solutions for each perturbation.

In contrast, extrinsic cues, such as changes in background color (Cunningham & Welch, 1994), cursor shape (Baldeo & Henriques, 2013), or object identity (Brown, Doole, & Malfait, 2011), often fail to support dual adaptation—unless they are made explicitly task-relevant. When extrinsic cues serve as the only indicator of the perturbation and are tightly coupled to task demands, they can support some degree of separation. For example, Hinder et al. (2008) showed that color cues could enable partial dual adaptation when each color reliably predicted a specific rotation. However, even then, learning was often shallow and inconsistent compared to when intrinsic cues were available.

More recent work has investigated whether tools—objects that inherently involve both extrinsic features (e.g., shape, color) and intrinsic properties (e.g., how they are manipulated)—can support dual adaptation. Heald et al. (2018) and Proud et al. (2019) showed that manipulating different control points on a single tool, each associated with a different force field, can yield distinct motor memories. McGarity-Shipley et al. (2020) extended this by demonstrating that dual adaptation can be anchored to specific “contact goals” combining a control point and a target. However, these studies often used large spatial or biomechanical differences—akin to training in different workspaces—which may have made the contextual separation easier.

What remains unclear is whether tools differing only in appearance (extrinsic cues) or only modestly in movement (subtle intrinsic differences) are sufficient to generate separate control policies and support true dual adaptation. This is particularly relevant in real-world scenarios where people frequently switch between tools that look and operate slightly differently (e.g., a fork vs. a spoon), yet still manage to avoid interference in performance. Understanding whether the motor system requires distinct movement dynamics—or whether visual identity can suffice—would clarify the kinds of contextual information that the brain uses to segregate motor memories.

The present study directly addresses this gap. Using immersive VR to simulate tool-based interactions, we manipulated the visual and motor properties of tool pairs to examine whether these features could serve as contextual cues for learning and switching between opposing visuomotor perturbations. Our aim was to determine whether extrinsic cues alone can support dual adaptation, or whether distinct movement dynamics are necessary to engage separate control policies and enable interference-free learning.

Methods

Participants

144 undergraduates (98 female, mean age = 21.98, SD +- 4.62) participated in and completed the study in one of four groups; Motor Incongruent (n = 40, mean age =22.41, SD +- 7.95), Motor Congruent (n = 40, mean age = 22.15, SD +- 8.27), Colour Control (n = 44, mean age = 19.56, SD, +- 5.47), and Single Adaptation (n = 20, mean age = 20.76, SD +- 3.98). All participants were right-handed and had normal or corrected-to-normal vision. Participation was voluntary and all participants gave informed consent prior to data collection. Participants were recruited through the Undergraduate Research Participant Pool (URPP) and received course credit upon completion of the experiment. The procedures used in this study were approved by the York Human Participants Review Sub-committee.

Experimental set-up

Participants were seated in a height-adjustable chair centered in front of a physical table that was visually rendered at the same height approximately 2 meters deep and spanned 3.5 meters wide. Throughout the experiment, participants wore a head mounted VR headset (Oculus Rift Consumer Version 1; resolution 1080 by 1200 for each eye; refresh rate 90 Hz). Three external sensors tracked the location of the headset and controllers (positional sampling rate 60 Hz, with an accuracy of <1mm). Before putting on the headset, participants were given the right controller and instructed to face straight ahead throughout the experiment. At the start of the experiment, participants positioned the hand-held controller at mid-chest level, aligned with the table height, and the experimenter then centered the visual stimuli around the controller's location. The VR environment was built in Unity 3D, using the Unity Experimenter Framework package to manage trial and block schedules for each group.

Stimuli

At the beginning of every trial, participants were presented with a tool, a ball (5 cm diameter), and a target (5 cm diameter cylinder), with a white scoreboard (20 x 30 cm) hovering near the end of the virtual table, as illustrated in Figure 3A-B and 4C. The target appeared 85 cm away from the ball-launch site, in 1 of 4 possible directions (75°, 85°, 95°, 105° in polar coordinates, as illustrated in Figure 3A). As illustrated in Figure 3D, the ball-launch point and the two flanking walls were positioned on the table, centered along the participant's midline and located approximately 30 cm in front of them.

The three possible tools are illustrated together in Figure 3D. These include a red paddle (right side) with a 6 cm diameter base, a brown curling rod (left side) featuring a 7 cm "pocket" to surround the ball, and a slingshot. To control for variations in "tool type" and movement requirements (see arrows in Figure 3C), each tool had a specific spawn location relative to the ball, as illustrated in Figure 4B and described in the next section. Similarly, the position of the timer bar (a horizontal green bar indicating countdown time) varied to ensure it did not obstruct the view of the tool, as described below. The flanking walls were included to ensure that the ball was launched from the same restricted area for all tools, and the tools themselves could not extend beyond this launching point.

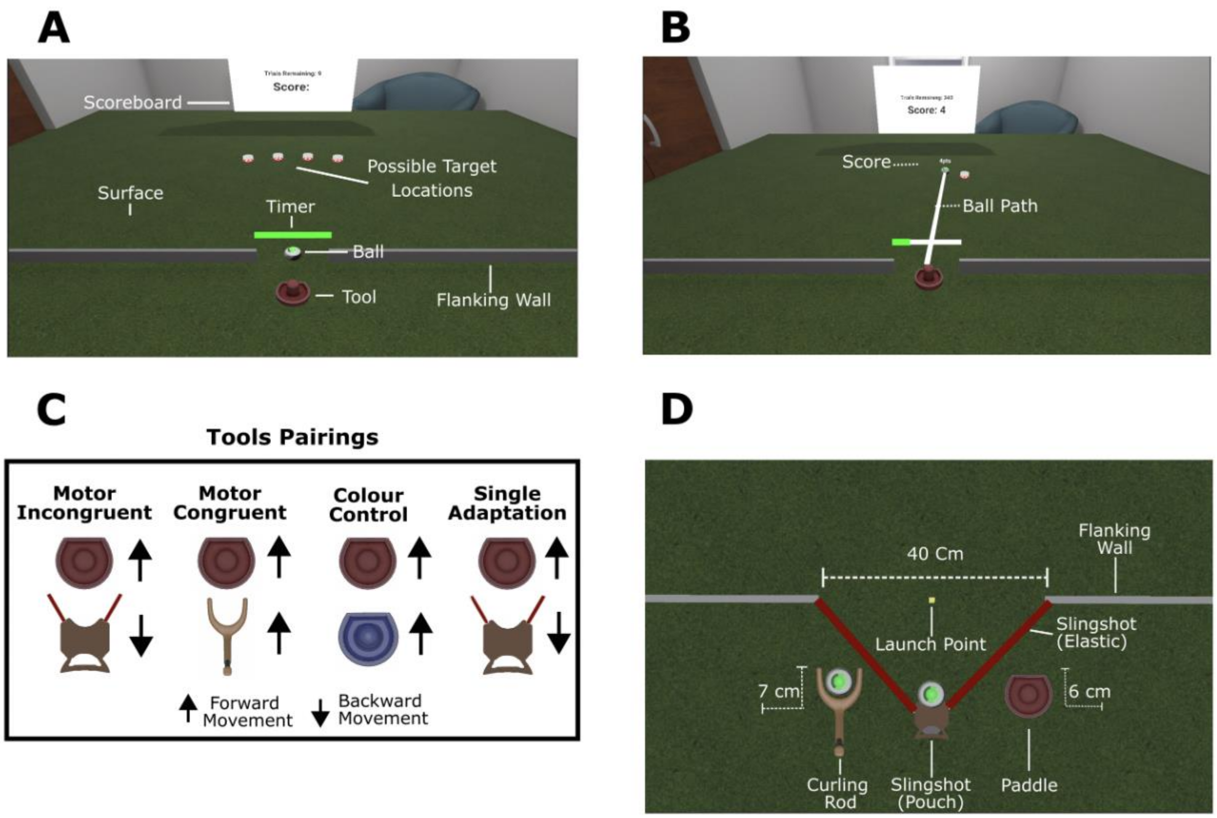

Figure 3. Experimental apparatus. A) Virtual environment in the VR experiment at the beginning of each trial. Once participants grabbed the tool, the timer would begin to deplete, prompting them to complete their shot toward the target. All four potential target locations — 75°, 85°, 95°, and 105° — are shown. B) The virtual environment in the VR experiment at the end of each trial. Participants score and trials remaining would be displayed on the scoreboard. In this example, the 75° target is shown. C) Illustration of the tool pairs used in each group. Arrows indicate whether a forward or backward movement was required to shoot the ball. Each Dual Adaptation group (Motor Incongruent, Motor Congruent, Colour Control) trained with two opposing rotations, each paired with a distinct tool. For the Single Adaptation groups (shown on

the right), only one tool and one rotation direction for a long training block. D) Rendering of the tools in the virtual environment.

Task and Tool types

The participant's task was to use the provided tool to shoot the ball toward the target. To begin each trial, participants moved the VR hand-held controller to the virtual tool. Since the controller and hand had no visible representation aside from the tool itself, it vibrated when brought within 1 cm of the tool. Upon reaching the tool, participants pressed and held the trigger button to "grab" it, beginning a countdown signaled by a green horizontal bar (Figure 3. A-B). The timer was set to 1 second (3 seconds during practice trials), signaling participants to quickly shoot the ball toward the target.

Shooting the ball involved intuitive, tool-specific movements. For the paddle (Figure 3A-D and 4C), the ball was positioned at the launch site, with the paddle placed 15 cm behind it. To shoot the ball, participants needed to perform a swift, forward motion with the paddle, striking the ball and propelling it toward the target.

The slingshot consisted of a white elastic band attached to the two horizontal flanking walls placed 40 cm apart, and a central brown pouch to hold the ball (Figure 3D and 4C). The elastic band of the slingshot appeared just behind the ball, which was positioned at the launch site. To shoot, participants pulled the sling, along with the ball, back 17 cm. Once released, the ball was propelled toward the target as it crossed the launch point. Since the ball was launched only after reaching this fixed backward distance, the velocity profile of the ball remained consistent across trials.

The curling rod appeared 15 cm behind the launch site, with the ball set at its vertex (Figure 3D and 4C). To shoot the ball, participants had to quickly push the rod forward to the launch site, where the ball would then be released. To ensure participants pushed the ball fully across the launch point, the gap between the walls surrounding the launch point (as shown in Figure 3D) was narrowed to 20 cm (compared to 40 cm for the motor-incongruent task). This reduced the solution space for the curling rod and ensured that all tools—paddle, slingshot, and curling rod—used the same launch point.

The ball's speed and direction were determined by the magnitude and direction of the paddle or rod at launch using the Unity software engine, PhysX, with a velocity cap of 22 cm/s. Since the slingshot only controlled the direction of travel, the default shot speed was fixed at 22 cm/s. The trial ended when the ball hit the target, slowed down to a speed of less than 1 cm/s, or travelled a radial distance of 120 cm from launch point. At this point, a white line appeared to indicate the ball path, providing participants with visual feedback on their accuracy (as shown in Figure 3B).

Moreover, to motivate participants, after each shot, they were awarded a score ranging from 0 - 10 depending on their minimum error, or the smallest distance between the ball and target during the trial. An additional 5 bonus points were awarded if participants hit the centre of the target. The overall score and the number of trials remaining was visually displayed on the scoreboard (Figure 3A-B). Missing the target by more than 20 cm or launching the ball after the timer depleted resulted in a score of 0.

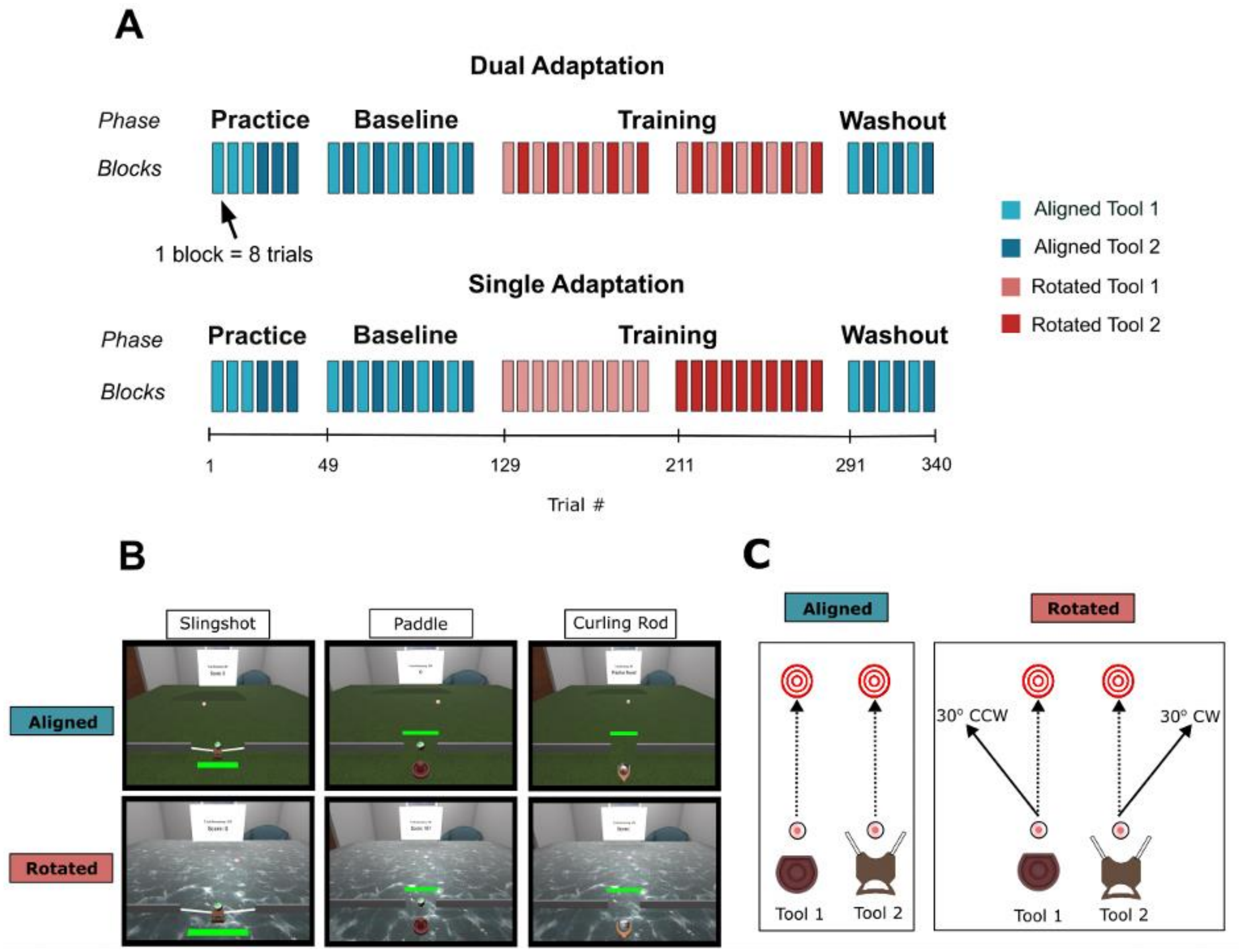

Figure 4. Layout of the experimental design. A) Participants in all groups completed 4 different experimental phases. Every vertical bar represents one block of 8 tool-specific trials. In Baseline and Washout phases, no perturbation was imposed on the ball (aligned trials). The Training phase involved a 30° angular perturbation on the ball (rotated trials). In the Dual Adaptation condition, participants alternated between tools every block. In the Single Adaptation condition, participants only alternated tools in the Baseline and Washout phases. During Training, these participants used one tool for 80 consecutive trials at a time. Tool order and rotation direction were counterbalanced across all participants. B) Visualization of aligned and rotated trials for the slingshot, paddle, and curling rod trials. C) Illustration of different trial types. In aligned trials, the ball rolls forward in the intended aiming direction, while in rotated trials the ball travels either 30° or –30° degrees depending on the tool used.

Groups

As will be described in further details below, these three distinct virtual tools (Figure 3C, 4C) were developed to serve as contextual cues that differed in both appearance and the type of pre-shooting movement they evoked (as illustrated in Figure 3C). For example, launching the ball with the paddle and curling rod involved a similar forward motion, whereas the slingshot required a backward pulling motion. These tools were paired in different combinations across groups to manipulate the congruency of the preparatory movements. In the Motor Congruent group, participants used a tool pairing consisting of the paddle and curling rod, which required similar launch movements and thus shared overlapping motor features across the two visuomotor perturbations. In contrast, the Motor Incongruent group used a pairing comprised of the paddle and slingshot, which involved clearly distinct pre-movement patterns. This distinct sensorimotor operation could potentially enhance the brain's ability to associate each tool with a separate visuomotor perturbations during interleaved training.

In these two main dual adaptation groups, each of the within-pairing tools were consistently associated with one of two opposing visuomotor rotations. This design allowed us to test whether differences in action preparation—in addition to visual tool identity—could facilitate the formation and retrieval of separate internal models during dual adaptation. To isolate the role of visual distinctiveness alone, a third dual adaptation group—the Colour Control group—used two differently coloured paddles with the perturbation direction cued by the colour of the paddle (red or blue). Finally, a Single Adaptation control group learned one rotation at a time, using the same tool–perturbation pairings as the Motor Incongruent groups, but without switching between perturbations. This allowed us to measure participants' typical learning rates without interference or contextual cue demands.

Procedure

All three dual adaptation groups trained with a pair of tools, each consistently associated with an opposing visuomotor rotation. The session began with trials in which the ball's motion was *aligned* with the direction of the tool's launch movement (Figure 4C, left) and thus unperturbed. To get people accustomed to the task mechanism, they practiced with these unperturbed trials for 24 trials per tool. This was followed by a Baseline phase consisted of 80 additional aligned trials (40 per tool) to assess initial baseline performance prior to introducing any perturbation. In the subsequent Training phase, a 30° clockwise (CW) or counterclockwise (CCW) rotation was applied to the ball, with each tool consistently paired with one of these misaligned directions (Figure 4C, right). During this phase, participants completed 160 rotated trials (80 per tool). For all three dual adaptation groups, the two opposing perturbations were interleaved in mini-blocks of 8 trials per tool (Figure 4A). To compensate for the visuomotor rotation introduced during the Training phase, participants had to adjust their hand movements in the direction opposite to the imposed rotation in order to accurately aim the ball at the target. Although the background texture changed between aligned and rotated trials (Figure 4B), participants were not informed about the presence of the rotation or the meaning of the texture change.

The final phase of the experiment, the Washout phase, was designed to assess initial aftereffects and early de-adaptation for all four groups. This phase consisted of 48 aligned trials (24 per tool) with aligned feedback. In-between phases, participants were given short rest breaks of 20 to 30 seconds, but were instructed to keep their VR headsets on throughout the session.

A fourth group completed the Single Adaptation (SA) condition, serving as a control. During the Training phase, participants in this group adapted to one tool and one visuomotor rotation at a time—either the paddle or the slingshot—during separate blocks of 80 trials (Figure 4A, bottom). Each participant completed 80 rotated trials with one tool and then switched to the other tool and the opposing rotation for another 80 trials, with order counterbalanced across participants. The Practice, Baseline, and Washout phases were identical to those in the DA groups. This design allowed us to compare learning in the dual adaptation conditions to that in single-tool (specifically the paddle), single-perturbation contexts, and to determine whether contextual cues such as tool identity and movement direction could effectively support concurrent learning of opposing motor mappings.

Experimental Design

This study used a between-subjects design with four groups of participants. Three groups completed dual adaptation (DA) conditions in which participants used two tools, each consistently associated with an opposing visuomotor rotation (CW or CCW) during the Training phase. Performance was evaluated by four measures; initial movement direction (measured at 3 cm from movement onset), angular deviation of the ball relative to the target, the switch cost– or the difference in angular error between the first trial of the current tool-specific block and the last trial of the previous tool-specific block– and the initial aftereffects measured during the Washout phase.

All four groups used the paddle as the common tool, which required a forward, push-like motion to launch the ball. Comparing the Motor Congruent and Colour groups allowed us to test whether distinct tool identities enhanced dual adaptation beyond visual colour cues. Comparing the Congruent and Incongruent groups allowed us to assess whether differences in launch movement direction further improved the separation of motor memories. In all DA groups, the tools were alternated every 8 trials (called blocks) throughout the Baseline, Training, and Washout phases, with the starting tool counterbalanced across participants.

Data Analysis

This study examined how contextual cues—specifically, tool identity (extrinsic cues) and tool operation (intrinsic cues)—influence the concurrent learning of tool-pair associations, each linked to a different visuomotor perturbation. By manipulating the congruency between the movement required to operate each tool and its visual identity, we aimed to determine whether extrinsic or intrinsic features, or their combination, support the formation of separate motor memories under dual adaptation conditions. To focus specifically on the effects of cue type under conditions requiring concurrent adaptation, some analyses included only the three DA groups. These groups differed in the type of contextual cue associated with the opposing perturbations.

The dependent variables were angular deviation (used to assess adaptation) during the Training phases and aftereffects (used to measure retention), both derived from the trajectory of the ball following launch. The primary performance measure in our analysis was angular error, defined as the difference between the ball's trajectory and the target direction. To facilitate comparisons between the different rotation directions, we standardized the two perturbations by reversing the sign of the launch angle errors for one of the rotations. This recoding allowed positive values to consistently reflect undercompensation, while smaller values indicated more successful adaptation. For reference, an angular error of 30 degrees would reflect a failure to compensate for the full imposed rotation, whereas values within ±3.3 degrees—corresponding to the diameter of the ball—were considered to indicate full compensation.

On each trial, we also calculated distance, or how far the ball traveled from the launch point. To control for potential biases in target direction and tool use, we calculated the median shooting errors for each target-tool combination during the Baseline phase and subtracted these values from the shooting errors in the Training phase. Trials were excluded from the analysis if they either failed to travel 20% of the required distance to the target (<17 cm) or had angular errors greater than ±60°. The distance criteria led to the removal of 96 trials, which reflect 0.07% of all trials in the main phases of each group. The angular criteria led to a removal of 586 trials (0.41%).

Before presenting the main analysis, we conducted preliminary checks for potential confounds, specifically tool order effects, that could have influenced our analytical approach. These results are reported here to justify the structure of the main analysis described in the next section.

To quantify the impact of tool-related cues on DA, we focused on performance with the red paddle, as it was the only tool common to all four tool pairings. This means that, for the purpose of this study, we did not analyze adaptation performance for the second tool of each pairing. However, we present the performance for both tools, across the main phases, averaged across participants, for all four groups (Figure 5). Notably, as expected, we did not observe substantial differences in tool performance during either the Baseline phase or the first block of eight Training trials, before the second tool and its associated perturbation were introduced. The mean performance for the paddle (always shown in purple in Figure 5) in each group falls within the 95% confidence interval of the other tool's errors. In fact, the 95% confidence intervals for each tool largely overlap during these trials, suggesting that performance errors did not differ significantly between the tools within each group. Furthermore, the overall accuracy of ball motion errors during the second half of the Baseline phase for each tool suggests that participants were generally able to use the tools effectively to shoot the ball to hit the 6-degree target (grey horizontal bar in Figure 5). In summary, people were able to operate the tools accurately in the absence of the imposing perturbation, and there were no tool-specific biases in performance when the perturbation was introduced.

In addition to participant performance with the second tool, we also quantified if tool order affected concurrent adaptation to both rotations. Indeed, we found that the order of the tool did have a small effect on the performance during training with the common paddle. Participants who trained with the paddle as the second tool, once the perturbation was introduced, showed an averaged shooting error of 34.23° for the first trial across the four groups, that was larger than those who trained with the paddle first (errors of 27.98°). This significant effect of tool order ($F_{(1,134)} = 7.478$, $p < 0.01$) suggests that training with the other tool (with the opposing perturbation) resulted in 7° of interference. However, given that there was no significant interaction with group ($F_{(3,134)} = 0.67$, $p = 0.57$), and the fact that tool-order (and its associated rotation direction) was counterbalanced across participants, we collapsed across tool orders for our main analyses. This approach simplifies the analysis, though it may reduce sensitivity to detecting significant differences, as variability within each block is partially influenced by order effects, particularly in the first trials of each block. However, such influences are an inherent challenge for the motor adaptation system to overcome during dual adaptation. Therefore, collapsing across multiple blocks provides a fair and balanced approach in the subsequent main analyses.

To determine whether there were any differences in angular error for the common paddle across the four tool-pairing groups, we used a 4 (group) x 2 (first, final) mixed-factors linear mixed effect model (LMER) to compare the (1) first and final trial and (2) first and final block, to assess total adaptation. When significant interactions were found, we then conducted a one-way between-subjects ANOVA across groups on errors in the first trial and again for the first block to confirm the absence of significant differences, given this early phase of Training. We explored interactions by performing a one-way between-subjects ANOVA across groups for errors produced during the final block of Training. Any significant main effect of block for the final trial or final block was further examined using Tukey post hoc comparisons.

Given that tools and their associated perturbations switched every 8 trials, we aimed to quantify both the amount of within-block learning during these 8 consecutive trials with the same tool and perturbation and the amount of adaptation retained following the intervening block of 8 trials with the other tool and opposite perturbation. To measure 'retention' between blocks, we compared the error in the first trial of each block (T1). To quantify adaptation by the end of each block, we used the error from the 8th and final trial of each block (T8). Although we plotted the errors for all initial (T1) and final (T8) trials across all ten consecutive blocks for each tool (in Figure 7A-C), to determine if errors significantly decreased over the course of Training, we focused our comparisons on the first block (Figure 6A, left) and the final block of Training (Figure 6A, right). We assessed this using two 3 (DA-tool groups) × 2 (block) LMERs: one for the initial trials (T1) and another for the final trials (T8) of the first and last Training blocks. Any significant group × block interaction was further examined using a one-way between-subjects ANOVA across groups for the first block—where no differences were expected—and for the last block, where any observed differences would be expected to drive the interaction. Any significant main effect of block for the final trial or final block was further examined using Tukey post hoc comparisons. If the cues specific to each tool pairing are deemed contextually relevant by the motor system, angular error should decline across the Training Phase at both T1 and T8.

Next, we tested whether tool identity and operation were sufficient to facilitate other measures of adaptation, such as aftereffects. To assess the presence of aftereffects, we compared the launch angle errors between the last block of Baseline and the first block of Washout across all tool-pairing groups using a 4 x 2 LMER on the common paddle. If a significant interaction was found, we conducted follow-up tests to determine which groups exhibited significant aftereffects (in the expected direction for tool-specific perturbation) by comparing the washout block with the baseline using paired t-tests for each group. To account for familywise error, we applied a Bonferroni correction for these four tests, using an adjusted significance threshold of $p = 0.0125$.

Results

General Results

To investigate whether tool-related cues are sufficient for dual adaptation, we will focus our analysis on the differences in total adaptation on the common paddles used across all four groups. However, we will first provide an overview of the general performance across all pairs of tools for each of the four tool pairings. After this general overview, we will present the statistical results for the common paddle tool.

Figure 5 illustrates angular ball-shooting errors, averaged across all participants, plotted across trials for each pair of tools for the four groups (A-D). To facilitate comparisons between the two tools, we plotted the last three Baseline blocks, all ten Training blocks, and all three Washout blocks for each tool as overlapping rather than alternating. However, as mentioned in the methods, half of the participants initially trained with the other tool before switching to the paddle, while the other half began with the paddle. To align the direction of error for both tools, the sign was reversed for the -30° tool for each participant. This format was applied to all figures.

As expected, there were no differences in angular error across any tool pairings in the Baseline phase ($p>0.18$; initial shaded area for each panel). When the visuomotor rotation was introduced, all groups showed similarly large initial deviations in the direction of the imposed perturbation, with no group differences in either the first trial ($F_{(3,138)} = 0.43$, $p = 0.72$) or first block of Training ($F_{(3,140)} = 1.53$, $p = 0.21$). This was also true when we analyzed paddle performance for just the three DA groups ($p>0.05$) (Figure 6B). Errors decreased within the first block of 8 trials during Training and continued to do so in each subsequent block. However, the zig-zag pattern of errors suggests that much of the within-block adaptation either partially or fully dissipated by the start of the next block with the same tool, indicating that the intervening tool disrupted retention. The 'cost' of switching tools, reflected by increased errors for the first trial of each block compared to the last trial of the previous block for the same tool, decreases in the Motor Incongruent group throughout the Training phase, while it remained consistent in the other two DA groups (Motor Congruent and Colour) (Figure 5). This improved retention of learning across blocks with intervening tools may have led participants in the Motor Incongruent tool-pairing group to show a greater overall reduction in shooting errors compared to the other DA groups. In the Single Adaptation group (Fig 5D), participants typically showed an exponential learning curve, with a steady reduction in error leading to near-complete compensation for the visuomotor rotation.

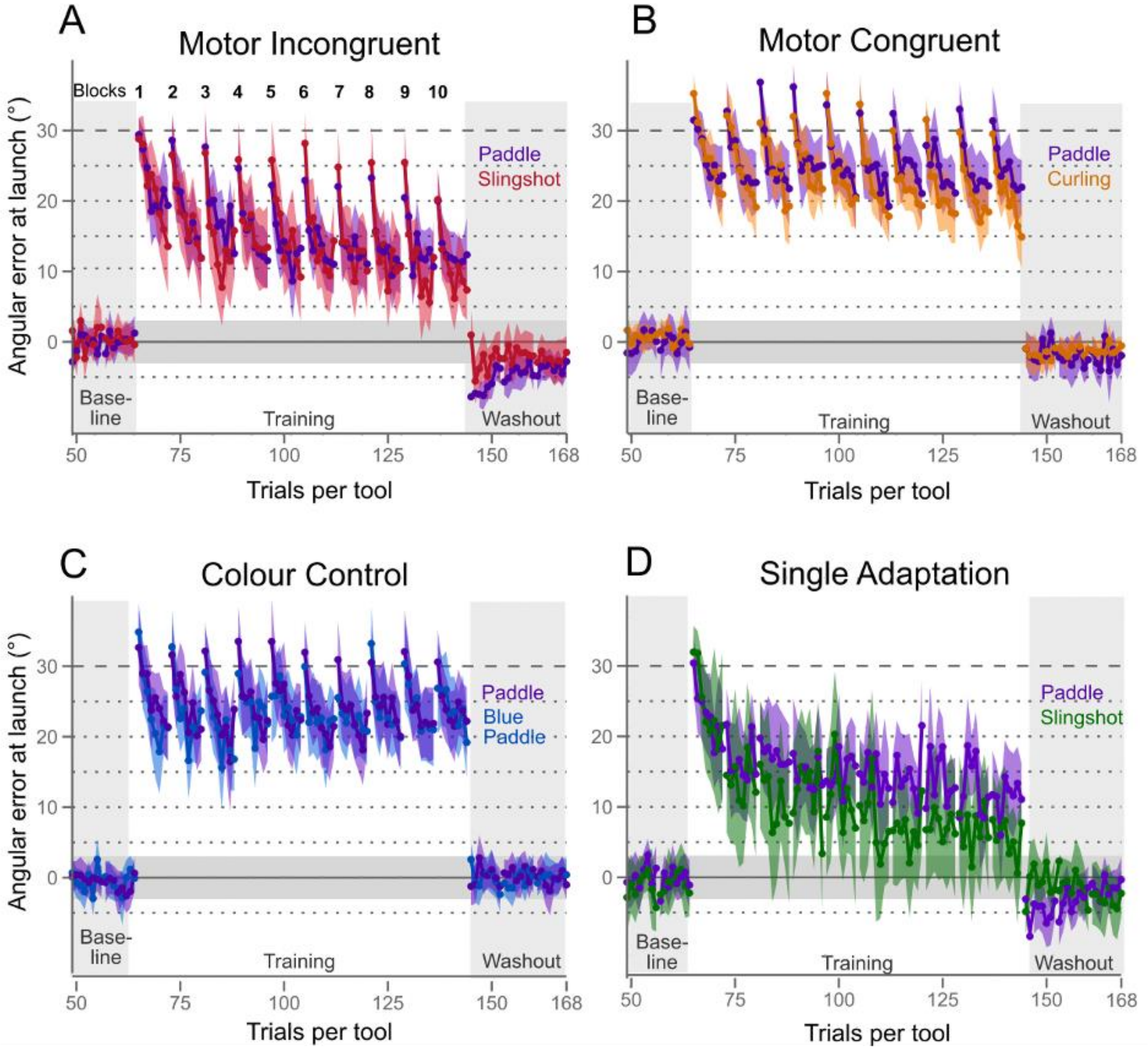

Figure 5. Launch angle error across tool trial numbers, averaged across participants for each tool pair, shown for the four groups: A) Motor Incongruent (purple for paddle, red for slingshot), B) Motor Congruent (purple for paddle, orange for curling rod), C) Colour-Control (purple for paddle, blue for blue paddle), and D) Single Adaptation (purple for paddle, green for slingshot). Although tools alternated in blocks of 8 trials, errors for both tools are plotted as overlapping across the corresponding trial number for each tool. These ten blocks are numbers on the top of panel A. The horizontal gray bar (±3° centered on the x-axis) indicates the range within which the 3.3° ball will hit the 3.3° target, relative to the launch point, for a successful hit. Shaded vertical areas on the left and right of each plot mark aligned trials, with the Baseline phase on the left and the Washout phase on the right. Only the final 24 trials of Baseline for each tool are displayed. The unshaded central area represents the Training phase, where ball motion was

deviated 30-degree, with block numbers for this phase shown above panel A. Although the rotations applied to the ball were in opposite directions for the two tools, the sign of one rotation was reversed to facilitate comparison. 95% confidential intervals are shown in matching colour for the two tools of each group.

Impact of Tool-Pairing on Adaptation Across Training

In this section, we will quantify the impact of tool-related cues on learning by analyzing error patterns during the Training phase for the red paddle, the tool that was common across all four pairings. This approach allowed us to directly compare the influence of extrinsic cues (tool identity) and intrinsic cues (the congruency of tool operation) on learning. Based on how paddle performance differs in the face of opposing perturbations, we can assess how the cues associated with the paired tool affect adaptation.

First, as expected, we found no differences across groups during the initial block of Training with the ball perturbation. While participants significantly reduced their launch errors between the first and last trials of this first Training block with the paddle ($F_{(3,275)} = 35.31$, $p < 0.001$), achieving approximately a 30% reduction in the initial ball perturbation, this reduction did not differ across groups ($F_{(3,275)} = 0.44$, $p = 0.719$). This lack of a group difference in the initial block of Training is consistent with the null effects reported in the methods when comparing across only the first trial or only the first block of errors when using the paddle across the tool pairing groups.

But what happens when participants adapt across 10 full blocks of 8 trials, alternating between the two tools with their opposing perturbations? In this case, we find evidence of dual adaptation, shown by a significant reduction in launch errors with the common paddle when comparing the very first and last trials (Figure 6A: $F_{(1, 138)} = 79.31$, $p<0.001$) and blocks (Figure

6B: $F_{(1, 147)} = 61.02$, $p<0.001$) of the entire Training phase. In both cases, the error reduction was significant, but the magnitude of the reduction varied significantly with the tool-pairing group (trial * group interaction: ($F_{(3,139)} = 2.84$, $p < 0.05$); block* group interaction: $F_{(3, 148)} = 13.33$, $p<0.001$). We find the same pattern of results for the post-hoc tests when comparing across the final block (Figure 6B) and trial (Figure 6A) of Training. In brief, while the errors by the end of Training were significantly reduced from the beginning for all four groups, adaptation in the Motor Incongruent group (red lines in Figure 6) did not differ significantly from the SA group (purple lines), indicating minimal interference when adapting to a second tool with incongruent operation ($p > 0.05$). Conversely, error reduction in both the Motor Congruent (different tool identity, orange lines) and Colour (different tool color, blue lines) groups was significantly smaller than in the SA group ($p < 0.001$), with no significant difference between these two DA groups ($p > 0.05$). In fact, at the block level, the lines corresponding to the first and last blocks remain flat for the Motor Congruent and Colour groups, indicating no overall reduction in errors across the ten blocks. The reduction observed at the trial level for these groups likely reflects adaptation specific to the final block of 8 Training trials. Together, these findings suggest that changes in tool color or identity were insufficient to achieve the same level of adaptation seen with a single perturbation.

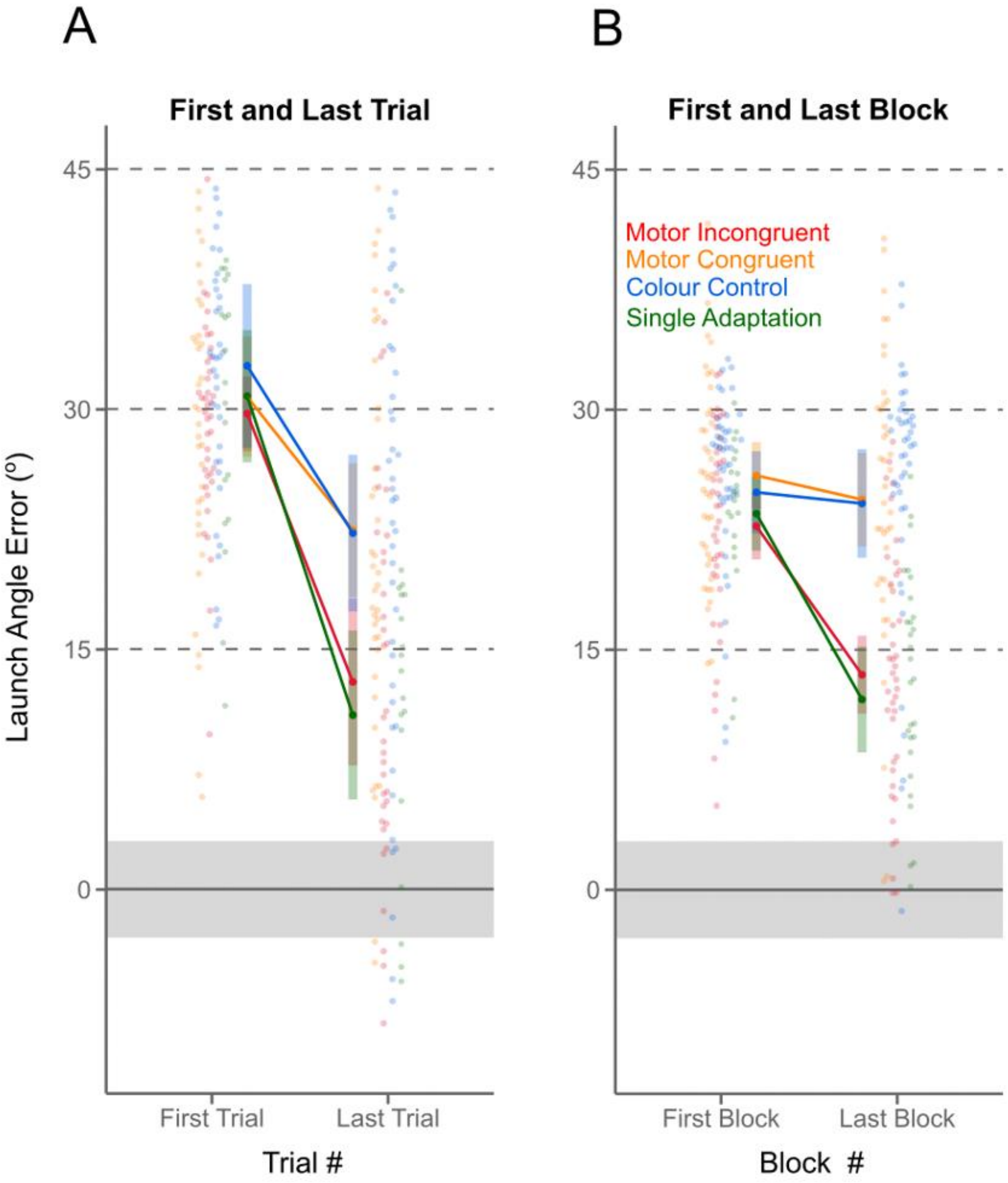

Figure 6. Angular launch error when adapting to the 30° rotation of ball direction using the paddle, shown for each participant (hollow circles) and for each of the four groups (full circle), with 95% confidence intervals across participants. (A) Launch errors averaged over the first and last trials of the Training phase. (B) Launch errors averaged over the first and last blocks of 8 trials during Training. Dark circles indicate the group mean error, with 95% confidence intervals across participants. The gray horizontal bar shows the range required for a successful hit, as illustrated in Figure 5.

Retention and Cumulative Adaptation Patterns in Dual Adaptation

Although our results suggest that only an incongruency in tool operation may provide a sufficient cue for DA, the zig-zag pattern in Figure 5 indicates that the adaptation process is more complex than this conclusion suggests. While ball deviation errors decreased over the 8 trials within each block (with the same tool and perturbation) for all ten blocks in the three DA groups, much of this within-block adaptation did not persist after switching to the opposing tool. To investigate this further, we separately compared the changes in ball deviations for the first trial (T1) for each block across all 10 blocks of Training (Figure 7 A-B) to measure the amount of adaptation retained after training with the intervening tool. To measure the extent of cumulative adaptation within each 8-trial block, we also compared the 8th or last trial for each block across Training (Figure 7C-D). To keep the ANOVA simple and interpretable, we focused on comparing the first and last (tenth) block of Training for only these first trials (Figure 7B) and last trials (Figure 7D) in the DA conditions, where the greatest error reduction would be expected.

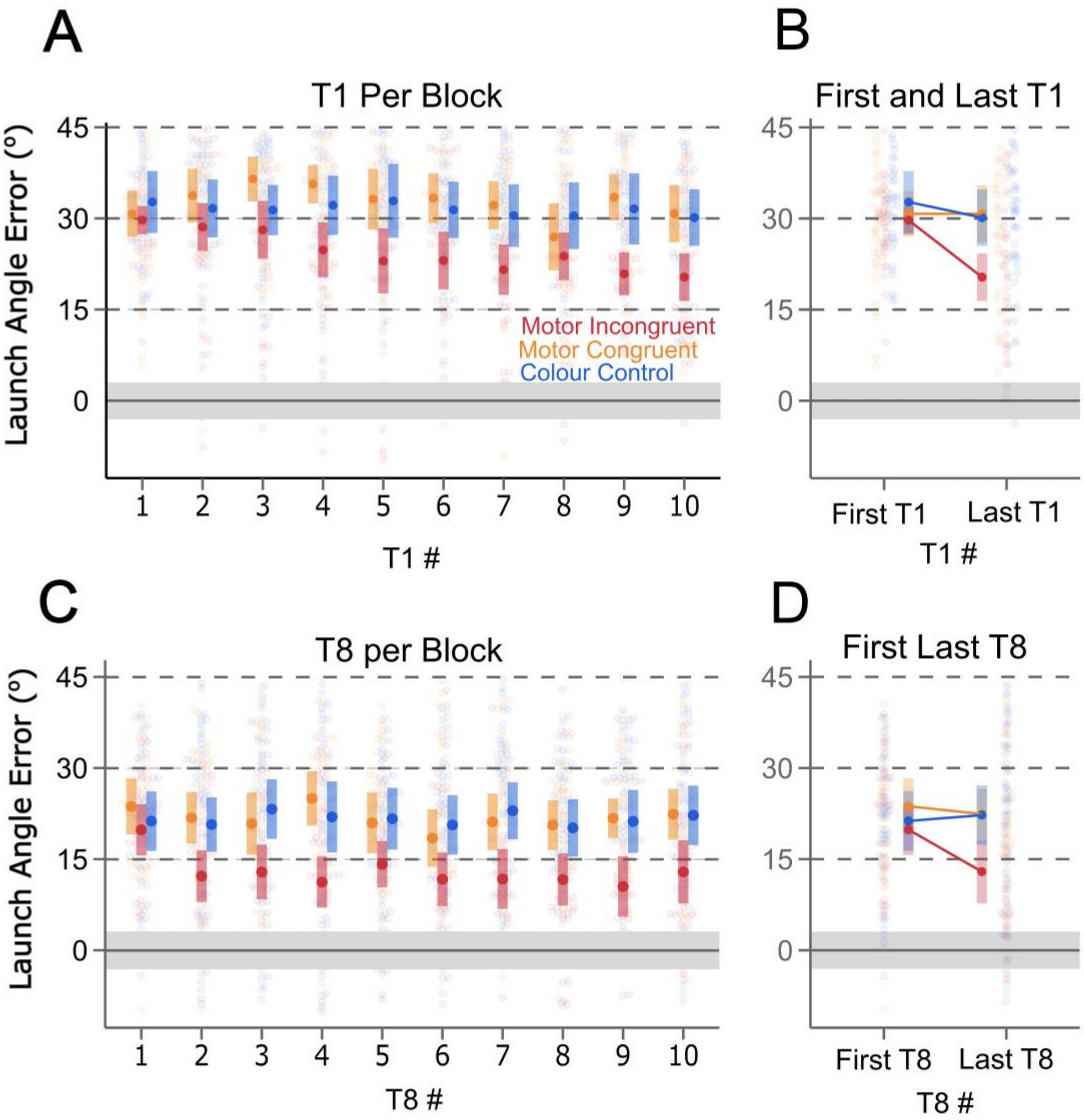

Figure 7. Launch errors for first trial (T1) (top row) and final trial (T8) (bottom row) of every block (A, C) and the first and last block (B, D) for each participant (hollow circles), and averaged cross participants (solid circles, with bars representing 95% confidence interval) for the three Dual adaptation groups; Motor Incongruent (red), Motor Congruent (yellow), Colour Control (blue). Grey horizontal bar as in Figure 5.

Comparing ball deviation for T1 in the initial block with that in the final block (Figure 7B) reveals a reduction in errors from block 1 to block 10 of the Training phase ($F_{(1,120)} = 7.12$, p

< 0.05; see Figure 7B). This suggests that some of the adaptation achieved within each of the ten blocks of eight trials is retained in subsequent blocks when using the same tool (see Figure 7A-B).

However, this reduction was group dependent (group*block interaction for T1: $F_{(1,120)} = 3.45$, $p < 0.05$). Given that this interaction could only be due to differences in the last block (since the paddle trials did not differ across group in the first block as described above), we ran a separate ANOVA on the final block of Training, where we confirmed a significant effect of groups on T1 ($F_{(2,119)}=6.87$, $p < 0.01$). Tukey comparisons suggests that this cross-block retention of learning is greater for the Motor Incongruent group than the Colour control (<0.01) and Motor Congruent group (<0.01). In fact, when examining Figure 7B, it appears that only the Motor Incongruent group (red) shows any reduction between the first and last block. Notably, in this group alone, the final data point falls below the confidence interval of the initial point.

When we look at T8 for the first and last block (Figure 7D), we failed to detect a difference in errors across blocks ($F_{(1, 120)} = 1.96$, $p=0.16$), nor a significant interaction between block and tool-pairing group ($F_{(1, 120)} = 1.84$, $p = 0.16$). This suggests that the cumulative adaptation observed within the very first block, before introducing the intervening second tool, is no greater than the adaptation achieved after nine additional blocks of training with the second tool. The lack of a significant interaction is somewhat surprising, given that errors appear to decrease for the Motor Incongruent group (red curve in Figure 7D) like it does for the first trial of each block (in Figure 7B). This discrepancy may be due to the challenge of detecting statistical differences in the presence of substantial inter-subject variability. Overall, tools with incongruent operations—providing both intrinsic and extrinsic cues—seem to have been sufficient for most participants to adapt to the tool-specific perturbations. By examining the adaptation patterns, we find that the dual adaptation observed in the Motor Incongruent group is largely driven by the retention of learning across the ten blocks, despite the introduction of the intervening second tool between each block.

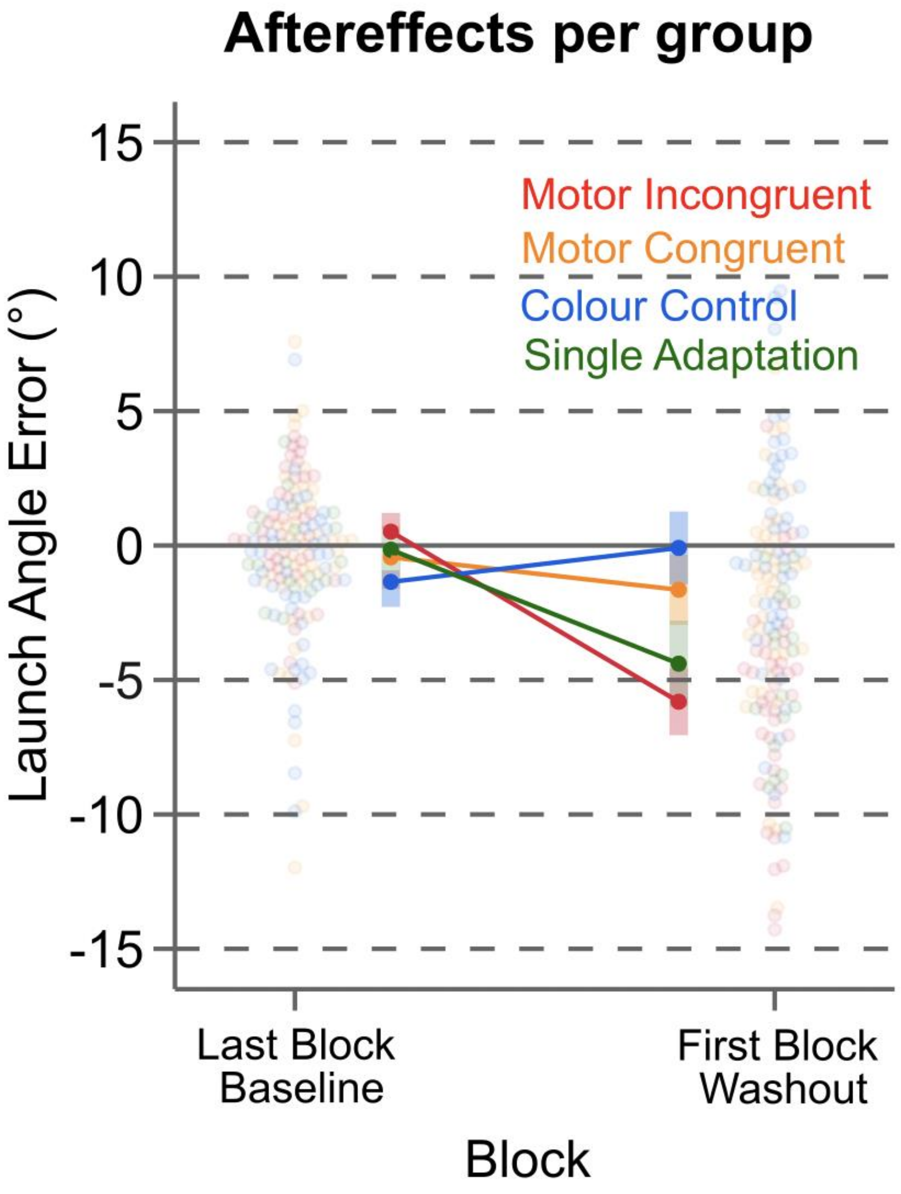

Figure 8. Mean launch error (filled circles) for paddle across all four groups across the Last block of Baseline and the First Block of Washout. Individual participant error (hollow circles) and 95% CIs (coloured rectangles) are shown for all trials.

Persistence of adaptation during Washout phase

To evaluate the effectiveness of the different paired tool cues on learning retention, we examined whether aftereffects persisted following Training. Specifically, we compared the first block of Washout trials—where the ball perturbation was removed after Training—to the last block of Baseline trials before the perturbation was introduced (Figure 8). Here we found small but persistent shooting errors in the direction consistent with adaptation, even in the absence of the perturbation ($F_{(3,140)} = 20.60$, $p < 0.001$). Paired comparisons using Bonferroni corrections found that only the Motor Incongruent ($p<0.001$) and SA ($p<0.001$) groups had significantly lower error in washout compared to baseline. Surprisingly the difference in error between these two groups was not significantly different ($p = 0.97$). Taken together, these results provide further evidence that different tools with incongruent movement directions may serve as effective cues, enabling levels of adaptation typically associated with a single tool and perturbation.

Discussion

The ability to learn and operate multiple tools with distinct control demands is a defining feature of human motor flexibility. To successfully interact with a variety of tools, the brain must maintain and selectively retrieve separate motor plans, or control policies, that specify how movements should be generated in each context. In this study, we asked whether the features of a tool—its visual identity (extrinsic cue) and movement dynamics (intrinsic cue)—can serve as contextual information for separating motor memories during dual adaptation to opposing visuomotor perturbations.

Using an immersive VR-based tool task, we compared learning across three dual adaptation (DA) conditions that systematically varied the cues available to distinguish tool-specific perturbations. Our findings demonstrate that only tool pairings involving distinct movement dynamics (i.e., the Motor Incongruent condition) supported successful dual adaptation. This group not only reduced reach errors over time, but also showed significant aftereffects, indicating the formation of separate internal models. In contrast, participants in the Color Control and Motor Congruent conditions—where tools differed only in visual identity or shared similar control dynamics—showed little improvement across Training blocks and no measurable aftereffects, despite reductions in error within each 8-trial block.

These results align with prior findings that intrinsic movement cues are more effective than extrinsic visual cues in supporting dual adaptation (Ayala & Henriques, 2021; Hamel et al., 2022). From a computational standpoint, learning two conflicting sensorimotor mappings requires that the brain maintain two distinct forward models and associated control policies, each predicting and correcting for a different visuomotor rotation (Wolpert & Kawato, 1998). In our task, the slingshot in the Motor Incongruent pairing introduced a distinct cardinal movement direction (pull vs. push), requiring a qualitatively different control policy than that used for the paddle. This difference appears to have been sufficient to prevent interference and support the retrieval of tool-specific motor memories.

By contrast, participants in the Color Control and Motor Congruent conditions experienced substantial interference, as reflected in the persistent "zig-zag" pattern of performance across blocks. Although within-block adaptation occurred, this learning failed to persist across tool switches—likely due to the reuse or blurring of control policies between tools. This is consistent with literature suggesting that when visual cues are not directly involved in movement generation, they are filtered out by the motor system as task-irrelevant (Forano et al., 2021; Tsay et al., 2022). Even in the Motor Congruent condition, where tools had distinct shapes but similar movement dynamics, adaptation was no better than when tools differed only in color. These findings highlight the limited utility of extrinsic cues when they are not tied to the motor execution itself.

Our findings align with and extend several strands of the dual adaptation literature. Previous work has consistently shown that intrinsic contextual cues—such as starting posture (Ayala, 't Hart, & Henriques, 2015), movement direction (Howard et al., 2013; Hamel et al., 2022), or the involvement of different muscle groups (Lee & Schweighofer, 2009)—can support dual adaptation. These cues are thought to directly engage distinct motor plans and thus enable the formation of separate internal models.

A particularly influential line of research by Howard and Franklin (Howard, Ingram, Franklin, & Wolpert, 2012; Howard, Wolpert & Franklin, 2013) demonstrated that lead-in movements—preparatory motions performed immediately before a primary movement—can serve as effective contextual cues for motor learning. For instance, in force field adaptation tasks, they showed that varying the direction or type (active, passive, or visual) of these lead-in movements allowed participants to form distinct motor memories for opposing force fields within the same workspace. They further showed that associating different follow-through movements—the motions executed immediately after the primary movement—with specific force fields could similarly reduce interference, suggesting that both preceding and succeeding movements can act as contextual signals for motor memory formation, or updating of the forward model. These studies collectively highlight the significance of movement context—both before and after the primary action—in shaping motor learning. Building upon this, Ayala &

Henriques (2021) showed that varying lead-in movements enabled participants to partly adapt to opposing visuomotor rotations within the same workspace. Similarly, McGarity-Shipley et al. (2020) found that different “contact goals”—i.e., combinations of target and control point on the same object—enabled distinct learning in a force field task. These studies, however, typically involved either large differences in workspace or specific goal targets tied to different spatial contexts.

What sets our study apart is the use of immersive VR to simulate tool-like interactions in a shared visual and spatial context, while varying tool cues that either preserved or altered tool-wielding dynamics. In contrast to earlier studies that used workspace separation (Woolley et al., 2007) or explicit instructions to isolate force field mappings (Heald et al., 2018; Proud et al., 2019), we show that motor-incongruent tool use alone—without spatial or instructional separation—is sufficient to enable dual learning. This suggests that the brain can dissociate conflicting sensorimotor mappings when the control policies required by each tool differ sufficiently, even when performed in the same visual environment.

Moreover, we demonstrate that visual tool identity alone, even when strongly associated with a particular perturbation, is insufficient to support dual adaptation unless the cue also alters the movement control requirements. These finding echoes long-standing conclusions in the literature about the limited role of extrinsic visual cues, particularly when they do not affect motor planning (Cunningham & Welch, 1994; Forano et al., 2021: Baldeo et al, 2013).

Our findings are consistent with recent VR-based studies examining the efficacy of visual object properties as contextual cues in motor adaptation. Modchalingam, Ayala, and Henriques (2024) conducted experiments to assess whether movement-goal relevant object-shape cues could serve as effective contextual signals during object-transport tasks in a virtual reality (VR) environment. Despite the presence of distinct object shapes to be transported to specific targets, these cues were not sufficient for context-specific dual adaptation. These results underscore that visual identity alone, even when associated with specific movement goals, may not be sufficient to elicit distinct motor adaptations unless the cues are intrinsically linked to the movement dynamics. Collectively, these studies, along with our findings, support the notion that task relevance—not perceptual salience—is the critical determinant of whether contextual cues enable the formation of separate motor memories.

However, our study adds a unique perspective by explicitly testing tools as contextual cues. While some prior work has used tool-like interfaces (e.g., a horizontal bar or paddle in Heald et al., 2018), few studies have systematically manipulated both tool identity and tool dynamics in a task that closely mimics naturalistic interactions. Our results suggest that when tools differ not only in how they look but in how they are wielded, they are more likely to engage distinct control policies, reducing interference and supporting robust dual adaptation.

Our aftereffects findings further underscore the importance of intrinsic movement cues. In both the Motor Incongruent and Single Adaptation conditions, participants exhibited significant reach deviations when the perturbation was removed for the common paddle—suggesting implicit motor memory formation. In contrast, no aftereffects were observed in the Color Control or Motor Congruent groups. Interestingly, the slingshot tool—despite enabling adaptation during Training—did not produce aftereffects in either the Dual Adaptation or Single Adaptation conditions. This may reflect the use of explicit strategies in response to its constrained movement pattern. The consistent draw-and-release action may have enabled participants to rely on simplified aiming heuristics, bypassing the need to update an internal model (Sheahan et al., 2016; Tsay et al., 2021). By contrast, the paddle, which allowed a range of movement magnitudes and directions, likely required more active recalibration and thus elicited aftereffects.

Our findings contribute to a broader understanding of how the motor system organizes and retrieves movement memories in multi-tool contexts. Tools are not merely objects with different visual forms—they are defined by the motor control policies required to use them. This suggests that the brain encodes tools based on their functional demands, not simply their appearance. Thus, tools that elicit distinct motor plans are more likely to be encoded as separate contexts during learning.

While our study demonstrates that distinct tool dynamics can facilitate dual adaptation, it is constrained by the specific design of the tool actions—particularly the slingshot's constrained motion path. This design choice may limit the generalizability of our findings to other tool-use scenarios. Future research should explore a broader range of tool-use dynamics, examining whether variations in movement parameters such as grip configuration, tool orientation, or movement timing can serve as effective contextual cues for dual adaptation. For instance, Proud et al. (2019) found that controlling different locations on a tool could lead to the formation of separate motor memories, suggesting that even subtle changes in interaction points may influence adaptation.

Additionally, our study did not incorporate tool-specific tactile information, which could play a significant role in contextualizing motor memories. Tactile feedback has been shown to enhance motor learning and retention, as evidenced by studies utilizing vibrotactile feedback to improve motor performance (van Breda et al, 2017). Integrating tactile cues into future experiments may provide deeper insights into the multisensory integration processes underlying tool-specific motor adaptations.

Conclusion

This study provides new evidence that movement-related features of tools, rather than visual appearance alone, support dual adaptation in immersive VR. When tools differ in how they are operated—especially in their control dynamics—the brain can form and retrieve distinct internal models with minimal interference. In contrast, purely visual differences fail to support dual learning unless they engage distinct control policies. These findings underscore the importance of task-relevant movement cues in shaping motor memory and provide a foundation for designing more effective learning, rehabilitation, and user-interface systems.

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