Task demands shift motor learning from adaptation to feedback control in a naturalistic bimanual task

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ABSTRACT

Most purposeful movements require the coordinated control of both hands, yet motor adaptation studies rely on highly constrained tasks that bear little resemblance to everyday bimanual actions. Here, we investigated how task demands shape control strategies during adaptation in a naturalistic bimanual object manipulation task. We tested 73 participants who lifted a virtual plate while we systematically distorted visual feedback of their right hand's movement, creating a sensory conflict between arms. Compared to unimanual, bimanual lifting shifted learning away from feedforward adaptation toward use of feedback control—participants moved more slowly with gradual speed scaling, developed compensatory hand adjustments, and showed smaller aftereffects. Relaxing precision demands improved success and reduced feedback reliance, while minimizing interlimb sensory conflict diminished compensatory adjustments and restored plate aftereffects to unimanual levels. Bimanual contexts create distinct learning environments where precision demands and interlimb sensory conflict independently shape control strategy; this may inform bimanual training protocols.

INTRODUCTION

Most purposeful human movements—whether manipulating objects, using tools, or performing skilled activities—depend fundamentally on the coordinated control of both hands. During such skilled actions, the motor system must maintain accuracy across changing external demands (object properties) and internal states (growth, injury) by continuously adjusting movements. One way the nervous system adjusts movements is through adaptation. Motor adaptation involves the gradual, trial-by-trial modification of movement in response errors from a perturbation. Learning through adaptation leads to persistent changes (aftereffects) when the perturbation is removed, requiring practice to de-adapt the newly learned pattern.[2] Adaptation is a key mechanism not only for maintaining accuracy but also learning new movement patterns.[3] Yet adaptation in bimanual contexts is far less studied than in unimanual contexts.[4] Addressing this gap is an important step for optimizing rehabilitation: understanding how best to train an impaired arm when it moves alone versus when both arms work together.

Bimanual tasks range from common-goal actions where both hands jointly control a single object (carrying a tray) to separate-goal actions where each hand controls different objects (unscrewing a jar lid).[5] The few studies that have examined common-goal actions suggest that the task goal determines how the motor system corrects[6–12] and adapts to perturbations.[13,14] During bilateral reaching with a shared cursor, perturbing one hand elicits bilateral corrections and adaptation; with separate cursors, responses remain confined to the perturbed hand,[13] resembling unimanual reaching.[6] The degree to which bimanual responses are shared or independent can be modulated by task demands:[15,16] when both hands control a shared cursor but one hand's movement has a bigger effect on where the cursor goes (i.e., higher gain), that hand takes over more of the control and moves more independently of the other.[16] Similarly, when one hand's movement consistently predicts what the other hand must do (i.e., right-hand movement predicts left-hand force), the brain stores a shared bimanual memory, but inconsistent predictions yield hand-specific memories.[17] Collectively, these studies suggest that task demands can shift control strategies in the bimanual context.

While previous studies establish principles of adaptation in the bimanual context, they offer limited insight into how these processes unfold in naturalistic tasks. Traditional adaptation studies use highly constrained tasks: participants control a single-point cursor using ballistic movements to reach abstract targets.[6–14,16] In contrast, everyday bimanual tasks involve manipulating objects and permit flexible motor strategies—slowing movements, making online corrections, or redistributing control across the hands to achieve goals. These naturalistic contexts create fundamentally different learning environments.[18–20] Rather than being forced to adapt, the motor system can shift between two strategies: adapting hand movements to predictively account for external demands or relying on sensory feedback to correct errors in real time. How adaptation unfolds during naturalistic bimanual tasks, where people can flexibly adjust their strategies, remains largely unknown.

Here, we investigated how task demands influence control strategies during adaptation in a naturalistic bimanual object manipulation task. Participants lifted a virtual plate of grapes while we systematically distorted visual feedback of their right hand’s movement, making it appear to move less than it actually did. We then manipulated three task dimensions to create distinct learning contexts: effector configuration (unimanual vs bimanual movements), precision demands (narrow vs wide target), and sensory conflict or consistency between hands (unilateral vs bilateral perturbation during bimanual movements).

Our overarching hypothesis was that these task demands independently influence distinct control mechanisms. We predicted that when both hands move together but only the right hand is perturbed (i.e., receive conflicting visual information), error attribution becomes ambiguous, which reduces motor adaptation and increases reliance on feedback-based corrections compared to unimanual movement. We further predicted that relaxing precision demands (wider targets) would reduce this feedback reliance, shifting control strategy toward adaptation, while restoring sensory consistency (bilateral perturbations) would eliminate sensory conflict and restore adaptation fully. By systematically examining how task demands shape learning in naturalistic bimanual coordination, this work contributes to an emerging framework for understanding real-world motor learning and provides principles for rehabilitating the impaired arm within its natural bimanual context.

RESULTS

We implemented a naturalistic bimanual object manipulation task in virtual reality to investigate how task demands influence motor learning when both hands work together. Participants wore a Meta Quest 2 VR headset with real-time hand tracking via a LEAP Motion controller (Fig 1a) to lift a virtual plate of grapes to a target zone at eye level (Fig 1b). The plate was positioned 30 cm below the target perch, which was surrounded by a target zone requiring precise plate placement (Fig 1c).

The basic experimental paradigm consisted of 260 trials across three phases with 30-second breaks every 30 trials (Fig 1d): baseline (50 trials) with veridical visual feedback, adaptation (150 trials) where visual gain was gradually reduced from 100% to 65% over 75 trials (ramp), then held constant for 75 trials (plateau), and washout (60 trials) where normal feedback was restored to examine aftereffects. As illustrated in example right-hand displacement traces in Fig 1e, participants moved their right hand higher and faster to counteract the reduced visual gain, with aftereffects persisting into early washout.

We first examined how the right hand adapts to visuomotor perturbations when coordinating with the left hand to control a shared object versus moving alone. In the bimanual-narrow group (n = 22), participants used both hands to lift a 26 cm plate to a 3 cm target zone while right-hand visual gain was reduced. In the unimanual-narrow group (n = 21), participants used only their right hand to lift a smaller 13 cm plate to the same target zone. To make task constraints more comparable between groups, we adjusted both the plate size and success criteria. The unimanual group used a smaller 13 cm plate (for more stable single-handed control) and needed only the plate center to reach the target zone. The bimanual group used a larger 26 cm plate but required both plate edges to reach the target zone. This stricter criterion for the bimanual group ensured that both groups faced similar constraints on the range of acceptable side-to-side plate tilts, thereby limiting redundancy in task solutions comparably across conditions.

Unimanual group was more successful than bimanual group.

During the learning block, success rate decreased in both groups as the perturbation was ramped down (Fig 2a), and the pattern of decrease mirrored the perturbation and was similar across both groups. Although target size was the same, success rate at the end of adaptation phase was significantly lower in the bimanual group compared to the unimanual group (mean difference = 38.5 ± 5.2%, t (41) = 7.35, p<0.001; Fig 2b).

Why was the success rate significantly lower in the bimanual group? The bimanual group had stricter requirements (both edges and center in target zone) compared to unimanual (center only). We quantified plate alignment error as the deviation from symmetry (bimanual) or from target center (unimanual), with values closer to 0 indicating better alignment (see Methods). The bimanual group's lower success rate was partly due to these alignment errors (r = 0.62, p=0.002; Fig 2c), whereas the unimanual group showed no such relationship (r = 0.19, p=0.41). The lack of correlation may be because, despite similar mean errors (bimanual: -1.5 cm; unimanual: -1.0 cm), the unimanual group's alignment was more consistent (range: -3.2 to 1.4 cm vs. -5.4 to 3.9 cm) and did not hinder success in most participants. In contrast, participants in the bimanual group more frequently failed to align the plate within the target, resulting in less success.

Participants could succeed by fully raising their hand to lift the plate center or they could tilt and rotate the plate to achieve this goal effectively decoupling hand and plate movement. We therefore examined both hand and plate displacement to understand each group's adaptation strategy.

Uni- and bimanual groups used different movement strategies to adapt to the perturbation.

Both groups learned by gradually increasing right-hand displacement over the adaptation phase (Fig 3a). However, by the end of adaptation, the unimanual group moved their right hand significantly higher than the bimanual group (43.8cm vs 40.1cm, t (41) = 5.6, p<0.001; Fig 3b). This difference in right-hand movement had functional consequences for plate control. In the unimanual group, participants who moved their right hand higher showed better plate center alignment within the target, i.e., less undershooting (r = 0.44, p=0.04; Fig 3c), suggesting they primarily relied on right-hand displacement to lift the plate. However, the bimanual group showed no relationship between right-hand displacement and plate alignment (r = -0.04, p=0.84) suggesting

that additional factors beyond right hand displacement contributed to the final plate alignment, which we explore next.

The bimanual group compensated for reduced right-hand displacement by using local hand adjustments rather than scaling up the entire movement. These compensations involved tilting or rotating the right hand to raise the plate center or adjust its orientation (Fig 3d). To capture right-hand compensation, we computed the difference between the plate center and right-hand displacement. The bimanual group progressively developed these hand compensations throughout adaptation (Fig 3e) and showed significantly more compensations than the unimanual group by the end of learning (2.7cm vs 0.6cm, t (41) = 4.7, p<0.001; Fig 3f), though some unimanual participants also used this strategy.

Unimanual group showed larger aftereffects in displacement than bimanual group.

Both groups showed aftereffects in right hand displacement (unimanual = 33.2cm, z = 5.0, p<0.001; bimanual = 31.3cm, z = 2.9, p=0.004), but these aftereffects were larger in the unimanual compared to bimanual group (mean difference of 2cm, t (41) = 2.5, p=0.012; Fig 4a). Only the unimanual group showed aftereffects in plate displacement (33.2cm, z = 5.7, p<0.001) while there were little to no plate aftereffects in the bimanual group (29.3cm, z = 0.22, p=0.82; mean difference of 3.8cm, t (41) = 6.5, p<0.001; Fig 4b). The left hand in the bimanual group also did not show aftereffects (Supplement S1).

Aftereffects in right hand and plate displacement seemed to last longer and reappeared after breaks in the unimanual group. In the bimanual group, those who adapted right hand displacement to a greater extent at the end of adaptation showed larger aftereffects during washout (r = 0.57, p=0.005). In the unimanual group, aftereffects were unrelated to end-of-adaptation displacement (r = -0.12, p=0.59) (Fig 4c) consistent with less between-subject variation in the learned state.

Both groups showed incomplete aftereffects relative to their learned behavior. The unimanual group adapted to approximately 44cm (Fig 3a) but showed average aftereffects of only 33.2cm (Fig 4a), while the bimanual group adapted to approximately 40cm (Fig 3b) but showed average aftereffects of 31.3cm (Fig 4a). This shows that right hand displacement magnitude alone does not capture the full extent of motor adaptation in this task.

Bimanual group used more feedback control than unimanual group.

So far, we have shown the bimanual group was less successful than the unimanual group. Additionally, the bimanual group exhibited more compensatory strategies and smaller aftereffects. These findings suggest that bimanual movements may rely more heavily on online feedback control rather than updating internal models through adaptation. If so, we would predict slower movements with more gradual movement scaling to allow time for online corrections in the bimanual group. Consistent with a feedback-control policy, the bimanual group showed lower peak speeds than the unimanual group. While groups did not differ at baseline, significant differences emerged during learning (mean difference ≈0.1m/s, p<0.05; Fig 5a).

Fig 5b shows example velocity traces from baseline (dashed) and adaptation (solid) trials. We see here that relative to baseline, the participant in the unimanual group showed a more pronounced increase in the initial phase of movement during adaptation, whereas in the bimanual group showed a more pronounced increase in the later phase of the movement. To capture this, we calculated early scaling as the ratio of average speeds between plate contact (vertical lines) and 20% of the normalized total distance (shaded regions), and overall scaling as the ratio of average speeds from plate contact to end of movement. The individual examples in Fig 5b showed similar early (1.55) and overall scaling (1.51) for unimanual but lesser early (1.18) than overall scaling (1.33) for bimanual movements.

Consistent with this, the group data revealed that the unimanual group showed relatively uniform scaling across the movement at the end of adaptation (early: 1.22 ± 0.05 to overall: 1.29 ± 0.05), whereas the bimanual group exhibited a more gradual increase in speed scaling (early: 1.15 ± 0.05 to overall: 1.29 ± 0.05), with significant difference between groups in this pattern (difference-in-difference = 0.06 ± 0.02, p=0.004; Fig. 5c). Despite intersubject variability, the bimanual group consistently increased their overall speed more than their early speed (change in speed scaling: 0.13 ± 0.04, z = 3.04, p=0.002; Fig 5d), suggesting that they continued to accelerate later in the movement rather than simply initiating faster. The magnitude of change in

speed scaling significantly predicted early speed aftereffects (r = -0.46, p=0.0021; Fig. 5e). Thus, speed scaling profiles revealed distinct control strategies between groups.

We reasoned that the bimanual group's poor performance, reliance on online feedback, and compensatory strategies could stem from two sources: frequent target errors due to precision demands, or interlimb prediction conflicts arising from asymmetric sensory prediction error between the hands. To distinguish between these possibilities, we conducted two control experiments—adaptation with a wider target and with visuomotor gains applied to both hands.

Wide target improved bimanual success and reduced feedback reliance, but hand compensations persisted.

If right hand compensations and feedback reliance were driven by target error, reducing precision demands of the task should alleviate these responses leading to more uniform scaling and improved performance like the unimanual group. Thus, we recruited a third group that learned right hand perturbations with a wider target (greater tolerance for target errors).

Widening the target substantially improved success rates in the bimanual group (mean improvement = 37.6 ± 5.8%, t (36) = 6.5, p<0.001; Fig 6a), with the wide target group achieving similar success rates as the unimanual group. Like the unimanual group, the bimanual-wide group showed relatively uniform speed scaling (Fig 6b), with minimal change between early and overall scaling (early: 1.24 ± 0.05 to overall: 1.23 ± 0.05) compared to the bimanual-narrow group (difference-in-difference = 0.14 ± 0.02, p<0.001; Fig 6c), suggesting less reliance on feedback control. These performance improvements occurred without changes to peak speed, movement time, hand, or plate displacement aftereffects (Supplement S2, p's>0.05) though as in the narrow target groups, uniform speed scaling continued to be associated with larger early speed aftereffects (Supplement S3). That is, the wide target improved performance and shifted control strategy from feedback-based to more feedforward (as reflected in early speed aftereffects) without affecting overall motor execution.

Despite improved success and reduced feedback reliance, hand compensations persisted (2.9 ± 0.32 cm). That is, people continued to compensate by tilting or rotating the right hand throughout adaptation (Fig 6d), reaching similar magnitudes to the narrow target bimanual group by the end of learning (mean difference = -0.19 ± 0.43cm, p=0.49; Fig 6d inset).

Bilateral gain perturbation reduced hand compensations and restored plate aftereffects.

If right hand compensations were driven by interlimb prediction conflicts, symmetric perturbation to both hands should diminish these responses. Thus, we recruited a fourth group who experienced gain perturbation to both hands and compared their compensatory response to the bimanual-narrow group that experienced right-hand perturbation only. Bilateral perturbation significantly reduced right hand compensation compared to right-only perturbation (mean difference = 1.2 ± 0.4 cm, t (35) = 3.2, p=0.002) though it did not eliminate this compensation entirely (mean ≈1.5 ± 0.29 cm, z = 5.2, p<0.001; Fig. 7a, b).

To further test the interlimb prediction conflict hypothesis, we examined how the left hand responded and how individuals coordinated compensations between hands to raise the plate center higher. We expected that when only the right-hand is perturbed, the left hand would compensate in the opposite direction to maintain the task goal. When both hands experience the same perturbation, they both should compensate in the same direction. Left hand compensations differed significantly between the two bimanual groups (mean difference = 3.7 ± 0.52 cm, t (35) = 7.1, p<0.001): right-only perturbation led to the hands compensating in opposite directions (orange, Fig. 7b, c), while bilateral perturbation led to both hands compensating in the same direction (green, Fig. 7b, c). Individual correlation analyses confirmed that greater right-hand compensation was associated with greater left-hand compensation in both groups (Supplement S4).

In addition to reducing compensations, the bilateral perturbation group showed significantly larger plate displacement aftereffects compared to the bimanual-narrow right-only perturbation group (mean difference = 2.8 ± 0.46 cm, t (35) = 6.1, p<0.001), but smaller than the unimanual right-only perturbation group (mean difference = 1.04 ±0.45 cm, t (35) = 2.3, p=0.02). Aftereffects in the right hand were similar to the bimanual-narrow right-only perturbation group (Supplement S5a-b, p>0.05). Because both hands were exposed to the perturbation, aftereffects were also observed for the left hand (Supplement S5c-d, p<0.05).

DISCUSSION

This study investigated how task demands shift control strategies during adaptation in a naturalistic bimanual object manipulation task. Participants lifted a virtual plate while we systematically perturbed visual feedback of their right hand's movement, requiring them to learn a new movement pattern. Three key findings emerged: First, compared to unimanual, bimanual coordination shifted motor learning from feedforward adaptation toward feedback control, particularly under stringent precision demands—participants relied more heavily on online corrections and developed compensatory hand adjustments rather than fully adapting their motor commands. Second, relaxing precision demands improved performance and reduced feedback reliance, but compensatory hand adjustments persisted and aftereffects were similar across groups. Third, reducing interlimb sensory conflict through bilateral perturbation diminished compensatory adjustments and partially restored adaptation. Together, these findings suggest that precision demands and interlimb sensory conflict shift how the motor system learns in a naturalistic bimanual task.

The differences between unimanual and bimanual groups are consistent with previous work showing that these contexts involve partially overlapping but distinct neural control processes.[21,22] However, prior studies examined separate-goal bimanual actions, where each hand moved to different targets (amplitudes or directions) or at different times. Less is known about adaptation when both hands control a single shared object. Shared bimanual control introduces unique challenges: mapping task goals to commands for each hand when multiple hand configurations can achieve the same outcome (redundancy) and assigning responsibility for errors when hands receive conflicting sensory feedback (sensory conflict). Our findings reflect these challenges: right-hand displacement predicted plate errors in the unimanual group but not the bimanual group (Fig 3c), where participants used a different strategy of redistributing control between hands and across multiple joints (hand compensations). The bimanual group also showed minimal aftereffects in plate displacement (Fig 4b)—consistent with exploiting multiple motor solutions—and greater reliance on feedback control and smaller right-hand aftereffects, indicating more ambiguous error attribution than unimanual control.

Previous work found that when controlling a shared cursor, both hands adapt to the same disturbance.[13,14] Our findings differ—we observed no left-hand aftereffects (Supplement S1) and hand compensations were in opposing directions (Fig 7c). This may stem from differences in how the shared object is represented: a single-point cursor, as studied in prior work, increases ambiguity in error attribution, causing both hands to adapt similarly, whereas plate tilt in our task provided an additional cue to right-hand as the source of errors, allowing more accurate error assignment. The opposing compensations further suggest that rather than adapting both hands to a shared error signal, the motor system flexibly exploits redundancy between hands to achieve task goals.[7] Thus, while bimanual control introduces ambiguity absent in the unimanual context, task-relevant cues like plate tilt may provide a more clear error source than in simpler single-point cursor paradigms. More broadly, our naturalistic task afforded flexible strategies (slowing movements, redistributing control, making online corrections), allowing adaptation and feedback control to interact naturally rather than being experimentally isolated as in traditional constrained paradigms using ballistic cursor movements.

Next, to examine what drives feedback reliance and compensatory adjustments, we conducted two control experiments: relaxing precision demands to reduce target errors, and perturbing both hands together to reduce sensory conflict.

Relaxing precision demands by widening the target improved success rates and reduced feedback reliance: the bimanual-wide group showed uniform speed scaling like the unimanual group. These improvements occurred without increases in peak speed or reductions in movement time, departing from the typical speed-accuracy tradeoff predicted by Fitts' law.[23] As in the narrow groups, the bimanual-wide group's more uniform speed scaling was associated with larger early speed aftereffects, however, contrary to our hypothesis, aftereffects in hand and plate displacement remained unchanged despite less feedback use and improved task success. This aligns with some previous work showing that implicit adaptation is insensitive to task success [24–27] but differs from others.[28–30] Notably, despite reduced target errors in the wide-target condition, compensatory hand adjustments persisted into washout. Those who relied less on compensations during adaptation (and more on wrist displacement) showed opposite-direction compensations in early washout (Supplement S6c),

suggesting they were reactively controlling for overshooting. This pattern indicates these compensations were driven by sensory prediction conflict between the hands rather than target errors.

When both hands experienced matched visual perturbations, compensatory adjustments were substantially reduced and plate aftereffects increased to levels similar to the unimanual group. The coordination pattern also changed: whereas unilateral perturbation produced opposing compensations between the hands, bilateral perturbation led both hands to compensate in the same direction (Fig 7c). Similar flexibility has been observed in other bimanual tasks where the unperturbed hand moved either opposite to or in the same direction as the perturbed hand depending on task goals.[7] Still, that some compensation remained may reflect biomechanical constraints of shoulder elevation during bimanual lifting. Together, these findings demonstrate how different task demands shift learning strategies in naturalistic bimanual tasks: precision requirements modulated feedback reliance, while sensory conflict influenced compensations and adaptation.

Several limitations warrant consideration. First, virtual environments can increase cognitive load, [31,32] potentially promoting more explicit learning strategies that are related to poor retention and context transfer.[33] Our participants did not report explicit awareness of the perturbation in our post-experiment debrief; still, cognitive load, particularly related to visuospatial processing, remains a concern. Second, our VR paradigm lacks the proprioceptive and haptic feedback present in real-world object manipulation; advances in haptic-integrated VR systems [34,35] may help address this. Third, we tested only neurotypical young adults in a single session, leaving open questions about retention, generalization, and applicability to clinical populations. To address this, we plan to test the feasibility of this VR-based bimanual training in stroke survivors.

Our findings have implications for how we might provide error-based training to the impaired arm, such as after stroke. For example, our results, particularly on restoring sensory consistency between the hands, suggest that error-based training of the impaired arm should account for existing asymmetries between the paretic and non-paretic arm in designing the perturbation to be applied to both hands. Key questions remain: Would stroke survivors, who often rely on compensatory strategies,[36] similarly recruit additional degrees of freedom such as the trunk? Would such compensations interfere with or support adaptation of the affected arm? How well does learning generalize to real-world bimanual tasks? Gamified VR training has the potential to increase engagement and facilitate high-volume practice in clinic and at home.[37–40] Whether error-based bimanual training in VR can improve function in clinical populations like stroke is a critical next question.

METHODS

Participants

Seventy-three neurotypical volunteers participated in one of four experimental groups (bimanual-narrow: n = 22; unimanual-narrow: n = 21; bimanual-wide: n = 16; bimanual-bilateral: n = 15; see descriptions below). All participants were naïve to the paradigm and completed one of the four conditions, except one who completed two (bimanual-narrow and unimanual-narrow). In accordance with the Declaration of Helsinki, study procedures were approved by the Johns Hopkins Medical Institutional Review Board (IRB00276939). All participants provided informed consent. Sixty-nine of the 73 participants (94.5%) reported being right-handed.

Setup and task

The task was implemented using the MovementVR platform[41] on a Meta Quest 2 VR headset with real-time hand tracking via a LEAP Motion controller. Hand tracking sampled on average at 90 Hz (range: 75-120), with LEAP Motion positional accuracy <1 cm under optimal conditions.[42,43] Data collection occurred in well-lit rooms to ensure optimal tracking quality. Participants lifted a virtual plate of grapes with both hands transporting it to a target perch at eye level. The target perch was surrounded by an orange zone requiring precise plate placement. Each trial began with participants placing both hands below a circular plate positioned 30 cm below the target. Participants then lifted the plate to the target zone with full visual feedback of their hands and the plate. Trials ended when the plate entered the target zone, with binary audiovisual feedback indicating success (green flash and a chirp) or failure (red flash and a squawk). Total trial time was capped at 30 seconds. Instructions emphasized keeping the plate level and reaching the target accurately. If the plate tilted beyond ~20°, grapes would slide off and the trial was unsuccessful. The virtual environments inside the game utilized Unity's physics engine to replicate naturalistic movement interactions: the grapes could slide off the plate, the plate could shift on the hands, and both the hands and plate could move freely in three dimensions. The friction coefficient between grape and plate, and plate and hand, was set to 0.6.

Learning paradigm

The experiment consisted of 260 trials across three phases (Figure 1D). During baseline (50 trials), virtual hand movements matched real movements. In the adaptation phase (150 trials), visual gain was gradually reduced from 100% to 65% over 75 trials,[44] then held constant for 75 trials. Gain perturbations were applied to wrist position at plate contact. A washout phase (60 trials) restored normal visual feedback to examine aftereffects. Rest breaks occurred every 30 trials to minimize fatigue. After the experiment, participants were asked open-ended questions to assess their awareness of the perturbation (e.g., “what do you think was happening?” or “was the game hard?” and “how was the game getting ‘harder’?”).

Experimental groups

Four experimental conditions were tested to examine different factors affecting bimanual motor learning:

1) *Bimanual-narrow*: Participants used both hands to lift a 26 cm diameter plate to a 3 cm target zone. Visual gain of the right hand was reduced from 100% to 65% during adaptation.
2) *Unimanual-narrow*: Participants used only their right hand to lift a 13 cm diameter plate to a 3 cm target zone. Visual gain of the right hand was reduced from 100% to 65% during adaptation.
3) *Bimanual-wide*: Identical to bimanual-narrow with visual gain of only the right hand reduced, but with a larger 6 cm target zone to reduce precision demands.
4) *Bimanual-bilateral*: Identical to bimanual-narrow but visual gain was reduced equally for both hands (100% to 65%) to eliminate interlimb sensory conflict.

Success criteria differed between unimanual and bimanual conditions. In unimanual, only the plate center needed to reach the target zone. In bimanual conditions, both left and right edges of the plate needed to reach the target zone to ensure participants experienced the full perturbation magnitude and maintained a level plate. The four versions of the game (bimanual-narrow, unimanual-narrow, bimanual-wide, bilateral-perturbation) used in this study can be found here: https://osf.io/8wbkh/ as PC executable applications.

Data processing and kinematic measures

Primary analysis focused on the y-axis (lifting direction). Trials with plate displacement less than 50% of the required distance were excluded, as were trials with technical errors (e.g., occasional loss in hand tracking, LEAP disconnection) or accidental plate drops (e.g., knocked over or flipped by hand on return). Time signals were linearly interpolated to yield 1000 samples. Hand and plate position data were filtered using a 4th-order Butterworth filter (5 Hz cutoff) and resampled to 1000 points via spline interpolation. Raw position data were corrected by subtracting initial values to normalize movement onset to zero. Velocity was calculated by differentiating position signals and smoothed for plotting using robust local regression (MATLAB Curve Fitting Toolbox: *smooth* function, 'rloess' method, 0.05 span). Movement onset was defined as first plate movement; offset as when the hand or plate reached maximum height.

For normalization and statistical analysis, the following epochs were defined in advance: baseline (last 10 trials before perturbation), ramp phase (first and last 25 trials), plateau phase (first 25 and last 50 trials), and washout (first 5 and last 10 trials). Larger windows were used where behavior was stable but noisy; smaller windows where rapid changes were expected.[45] Key measures included: (1) Success rates calculated as frequency of reward outcome within predefined epochs. (2) Right-hand position measured as maximum vertical displacement from movement onset to offset. (3) Plate alignment error measured as positioning accuracy at target entry and was calculated differently for bimanual and unimanual conditions to capture the relevant source of error in each task. For bimanual conditions, this was calculated as the height difference between right and left plate edges based on final plate orientation (pitch, roll, yaw), with positive values indicating the right edge was higher than left edge. For unimanual conditions, plate alignment error was the vertical deviation of the plate center from the target height. (4) Hand compensation calculated as the difference between plate center displacement and seen right wrist displacement, capturing local adjustments by tilt or rotations. (5) Early and overall speed scaling measured as average hand speed at 20% of total vertical displacement and across the entire movement, respectively, both normalized to individual baseline performance. Early speed scaling used the 20% spatial threshold to accommodate inter-individual displacement variations. Complete compensation for the 65% visual gain would require 1.538× scaling above baseline.

Statistical analysis

All statistical analyses were performed in R (version 4.5.1) and visualization using the *ggplot2* package (version 4.0.0). Statistical significance was set at $\alpha = 0.05$ for all analyses. All measures were summarized as subject-wise means for predefined epochs for further analyses. Primary comparisons focused on end of plateau (end of adaptation) and start of washout (aftereffects). Missing trials were removed from analysis; at the end of adaptation, participants were missing a median of 4 trials (IQR: 2–7) out of 50; missingness at start of washout was negligible. All data reported in results and figures are as mean ± standard error unless otherwise specified.

A priori hypothesized group differences in epoch-averaged measures were assessed using robust linear models to minimize the influence of outliers (using the 'rlm' function in the *MASS* package version 7.3.65), which downweights outliers rather than excluding them.[46] Comparisons included: unimanual-narrow versus bimanual-narrow for success rate, right-hand displacement, hand compensation, and aftereffects; bimanual-narrow versus bimanual-wide for success rate, peak speed, movement time, aftereffects, and hand compensation; and bimanual right-only perturbation versus bimanual bilateral perturbation for hand compensation and plate aftereffects. To determine whether hand compensation was significantly different from zero within each group or condition, estimated marginal means were tested against a null value of zero. An additional comparison examined plate aftereffects between the bimanual bilateral perturbation group and the unimanual group to assess whether bilateral perturbation restored adaptation toward unimanual levels. Estimated marginal means and pairwise contrasts (using the *emmeans* package version 1.11.2.8) [47] were computed, with t-statistics and residual degrees of freedom reported.

To examine how groups differed in peak speed and movement speed scaling strategy across learning, we used robust linear mixed-effects models with subject as a random intercept to account for repeated measures (using the *robustlmm* package version 3.3.3).[48] For peak speed, group and learning epoch were included as fixed effects, with pairwise contrasts comparing unimanual-narrow versus bimanual-narrow at each epoch. For

speed scaling, trial-wise speed data were modeled with group, movement phase (early: 20% of total displacement versus overall: 100% of total displacement), and learning epoch as fixed effects. The group-by-movement-phase interaction tests whether the change from early to overall scaling (i.e., speed scaling change) differs between groups. Difference-in-difference contrasts compared this scaling change between groups at each learning epoch. Separate models compared: unimanual-narrow versus bimanual-narrow, and bimanual-narrow versus bimanual-wide. P-values were Bonferroni-corrected across the five learning epochs (baseline through end of plateau). Asymptotic z-tests are reported for these contrasts. To confirm group differences at the end of adaptation, we additionally fit robust linear models on epoch-averaged scaling change scores. Estimated marginal means for epoch-averaged scaling change scores were tested against a null value of zero to determine whether each group showed significant speed scaling change at the end of adaptation.

Relationships between continuous variables were assessed using Pearson correlation coefficients, computed separately for each group. Correlations examined: (1) plate alignment error and success rate at the end of adaptation, (2) right-hand displacement and plate alignment at the end of adaptation, (3) right hand displacement magnitude at the end of adaptation and aftereffects at the start of washout, and (4) speed scaling change at the end of adaptation and aftereffects in early speed scaling at the start of washout.

Author Contributions

R.V. designed the study, collected and analyzed the data, performed statistical analyses, prepared all figures, and wrote the manuscript. C.R. developed the VR task methodology, contributed to study design, and data interpretations. L.A.M. contributed to study design and data interpretation. A.J.B. secured funding, supervised the study, and contributed to study design and data interpretation. All authors reviewed and revised the manuscript.

Data and Code Availability

Data and code to reproduce all the figures presented in this manuscript are available here: https://github.com/rinivarg/VRAdapt-Adults/tree/main

Acknowledgements

This work was supported by the following funding sources: grants from the National Institutes of Health T32 HD007414 and R35 NS122266 to A.J.B. We thank Naser Al-Fawakhiri for helpful comments on earlier versions of this manuscript.

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Figure 1. Setup and experimental paradigm. **(a)** Participants wore a Meta Quest 2 headset, on which a LEAP motion controller is mounted. **(b)** Game view shows real-time tracking and rendering of embodied hands and virtual objects. **(c)** Lifting task parameters including distance to target, target tolerance (narrow, 3 or wide, 6 cm in the two bimanual groups), and plate width (bimanual, 26 or unimanual, 13 cm). **(d)** Perturbation schedule showing gradual ramp down of visual gain of right-hand y-position to reach a maximum size of 65% of the 'real' right hand's y-position (green line). The dark gray line and shaded region are the expected responses and success zone in response to the gain perturbation. **(e)** Right hand vertical displacement from one participant showing canonical response to the gain perturbation. As perturbation ramps up (2), right hand displacement increases compared to baseline (1, dashed line) but with similar initial trajectory. By the end of the adaptation phase (3), right hand displacement increases further, notably with steeper early slopes indicating faster movement speeds. Initially during washout (4), changes in early trajectory persist though the hand may correct online to avoid overshooting and therefore not reach as high.

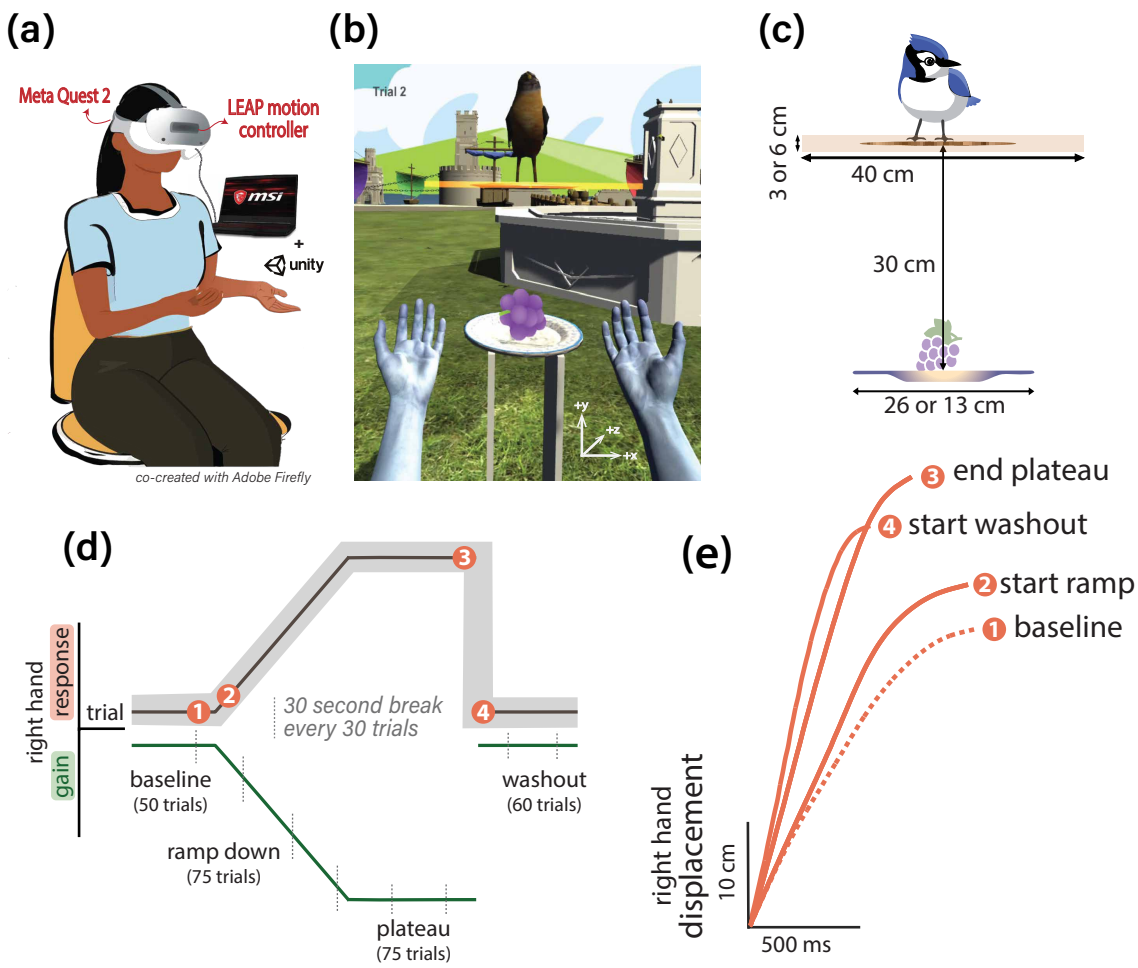

Figure 2. Unimanual group was more successful than bimanual group. **(a)** Success rate across epochs showing a decrease during the adaptation phase (tick marks correspond to start ramp, end ramp, start plateau, and end plateau) which persists into the start of washout, but is restored back to baseline levels by the end of the washout phase. **(b)** Success rate was higher in the unimanual group compared to the bimanual group at the end of adaptation. **(c)** Success rate was correlated with plate alignment errors at the end of adaptation in the bimanual group but not in the unimanual group. Error bars represent SEM.

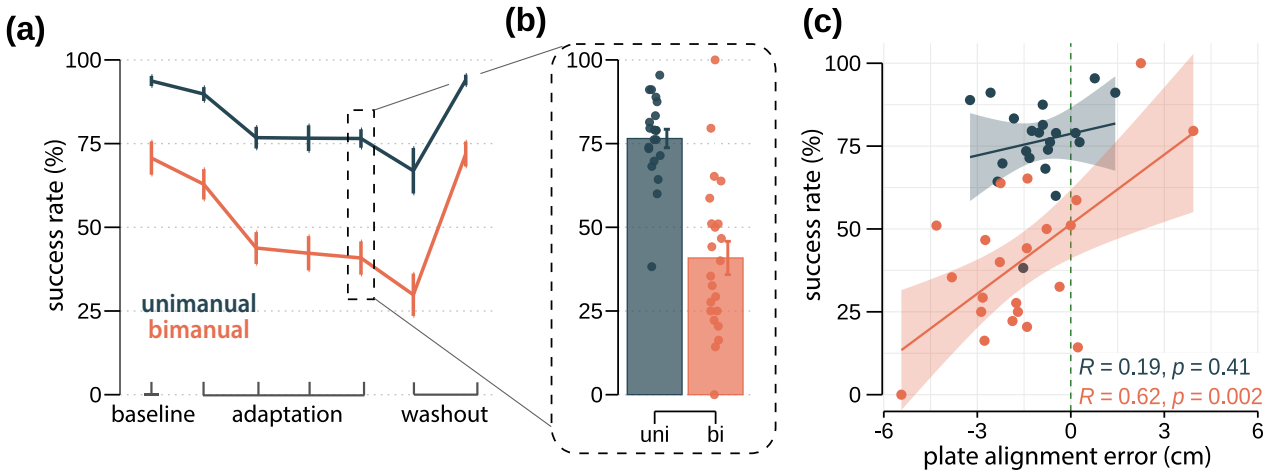

Figure 3. Right hand displacement and compensation strategies during adaptation. **(a)** Trial-by-trial group averages for right hand displacement (deviation from baseline position) during baseline and adaptation phases. **(b)** Epoch average at the end of adaptation phase showing higher right-hand displacement in the unimanual compared to the bimanual group. **(c)** At the end of the adaptation phase, right hand displacement correlated with plate alignment in the unimanual group but not in the bimanual group, suggesting the bimanual group used alternative strategies beyond displacement to achieve plate alignment. **(d)** Example of compensatory wrist adjustment in bimanual lifting: when the seen right hand is below plate center (white square), the learner tilts the wrist to raise the right plate edge and maintain plate alignment. **(e)** Trial-by-trial averages for right hand compensation (vertical distance from plate center to seen right wrist position) showing progressive increase over the adaptation phase. **(f)** Epoch average at the end of adaptation phase showing larger right-hand compensation in the bimanual compared to the unimanual group, with considerable variability among participants in both groups. Error bars/shading represent SEM.

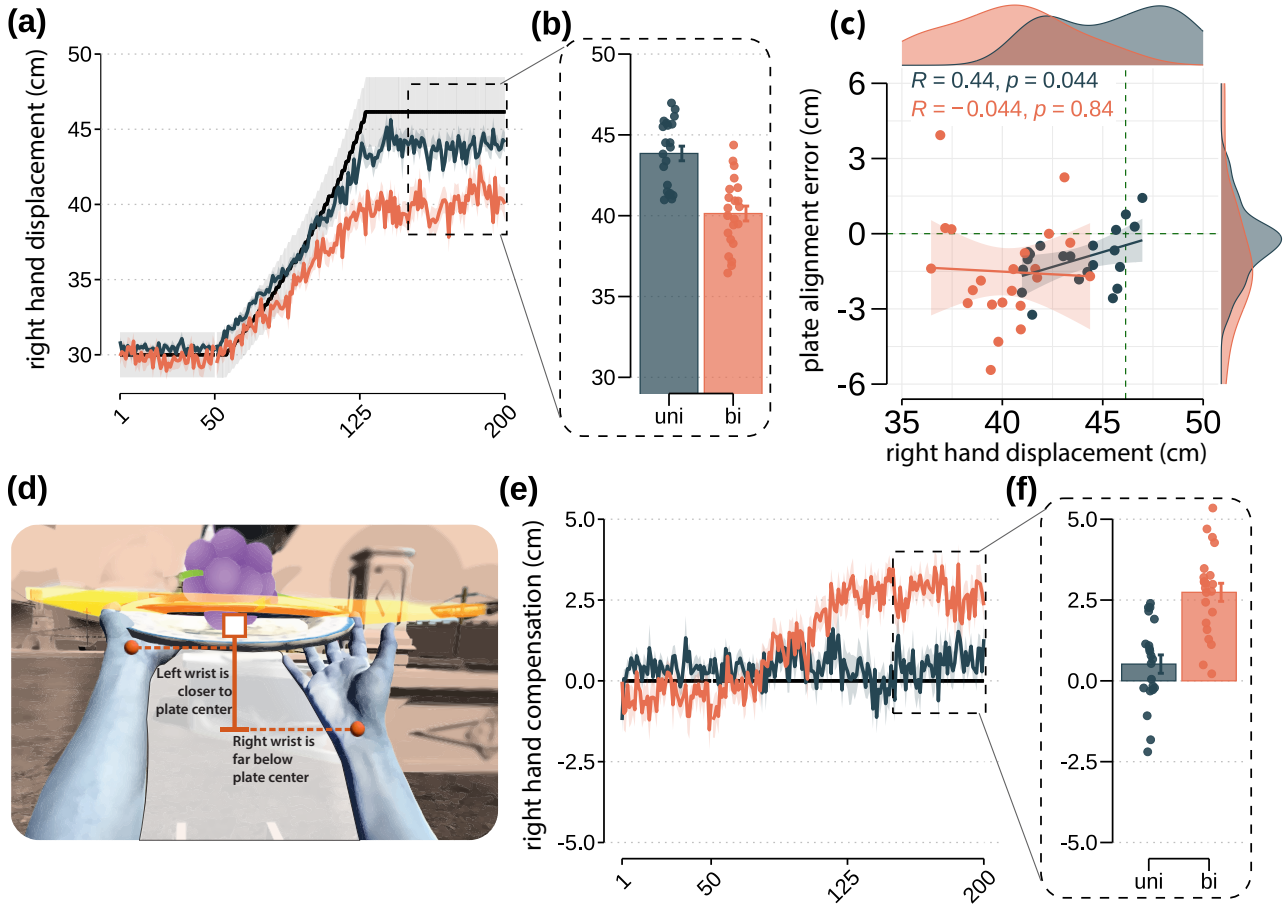

Figure 4. Unimanual group showed larger aftereffects in displacement than bimanual group. **(a)** Trial-by-trial group averages for right hand displacement during washout showing aftereffects in both groups, with larger aftereffects in the unimanual group. Inset shows epoch average at the start of washout. **(b)** Trial-by-trial group averages for plate displacement during washout showing aftereffects in the unimanual group but minimal aftereffects in the bimanual group. Inset shows epoch average at the start of washout. **(c)** Right hand displacement at the end of adaptation correlated with aftereffect magnitude at the start of washout in the bimanual group but not in the unimanual group. Error bars/shading represent SEM.

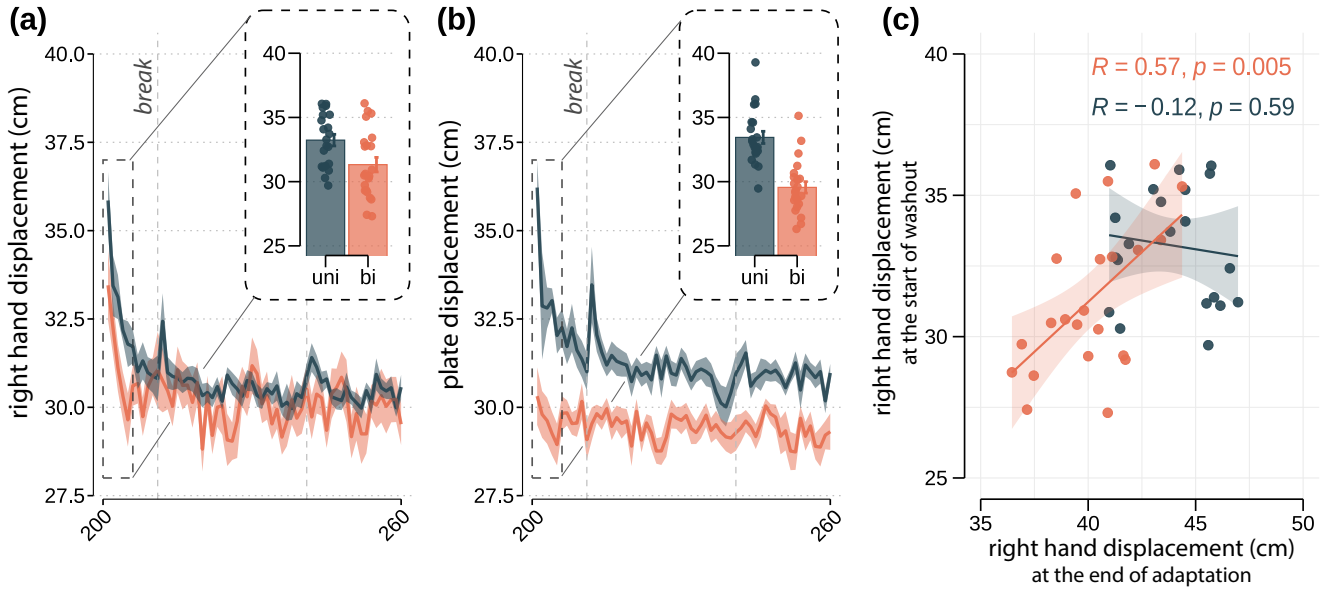

Figure 5. Bimanual group used more feedback control than unimanual group. **(a)** Epoch average for right hand peak speed at the end of adaptation showing lower peak speeds in the bimanual compared to the unimanual group. **(b)** Example velocity profiles from individual participants showing baseline (dashed) and adaptation (solid) trials. Vertical line indicates plate contact, where the visuomotor gain is applied; shaded region following plate contact indicates early phase (plate contact to 20% of normalized total movement distance) used for early speed scaling calculations. Speed scaling (formulas shown) quantifies the increase in speed during adaptation relative to baseline for the early phase of the movement and the entire movement (overall). The unimanual participant scaled their speed in the early phase and maintained that scaling throughout the movement (uniform scaling: 1.55 early, 1.51 overall), whereas the bimanual participant scaled their speed less in the early phase and increased scaling later in the movement (gradual scaling: 1.18 early, 1.33 overall). **(c)** Trial-by-trial group averages for early (lighter shade) and overall (darker shade) speed scaling across all phases showing patterns of uniform and gradual speed scaling in the unimanual and bimanual group, respectively. **(d)** Epoch average for change in speed scaling (overall minus early) at the end of adaptation showing greater change in the bimanual compared to the unimanual group, with considerable variability among participants in both groups. **(e)** Change in speed scaling (indicative of online feedback use) was negatively correlated with early speed aftereffects at the start of washout. Error bars/shading represent SEM.

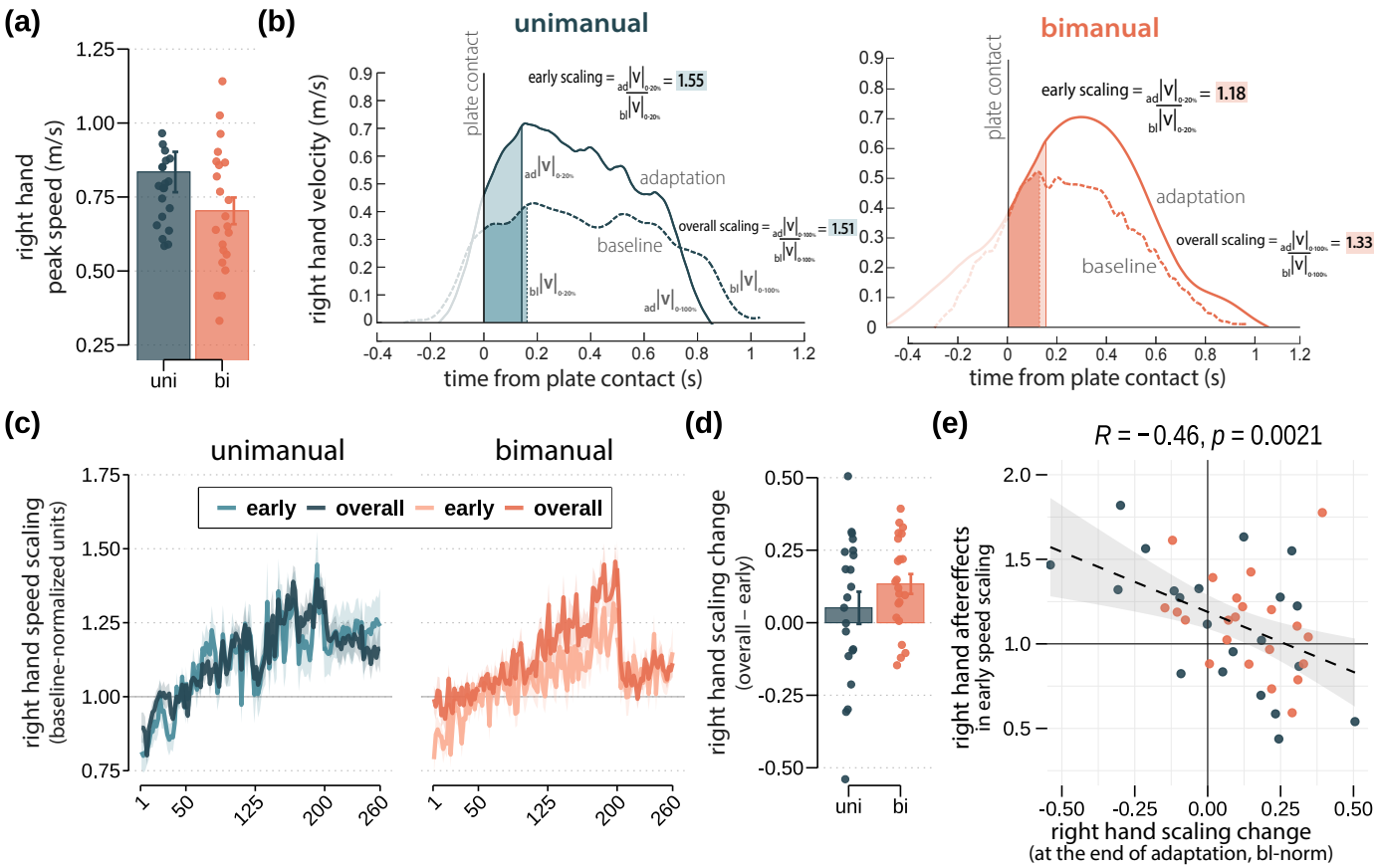

Figure 6. Wide target improved bimanual success and reduced feedback reliance, but hand compensations persisted. **(a)** Epoch average for success rate at the end of adaptation showing higher success in the bimanual-wide group compared to bimanual-narrow group, with bimanual-wide resembling unimanual group. **(b)** Example velocity profile from a bimanual-wide participant showing baseline (dashed) and adaptation (solid) trials. Shaded region indicates early phase used for speed scaling calculations. This participant showed uniform scaling (1.75 early, 1.75 overall), similar to the unimanual pattern. **(c)** Epoch average for change in speed scaling (overall minus early) at the end of adaptation showing smaller change in the bimanual-wide group compared to bimanual-narrow group, with bimanual-wide resembling unimanual group. **(d)** Trial-by-trial average for right hand compensation showing progressive increase over the adaptation phase. Inset shows epoch average at the end of adaptation with similar compensation magnitudes between the bimanual groups. Error bars/shading represent SEM.

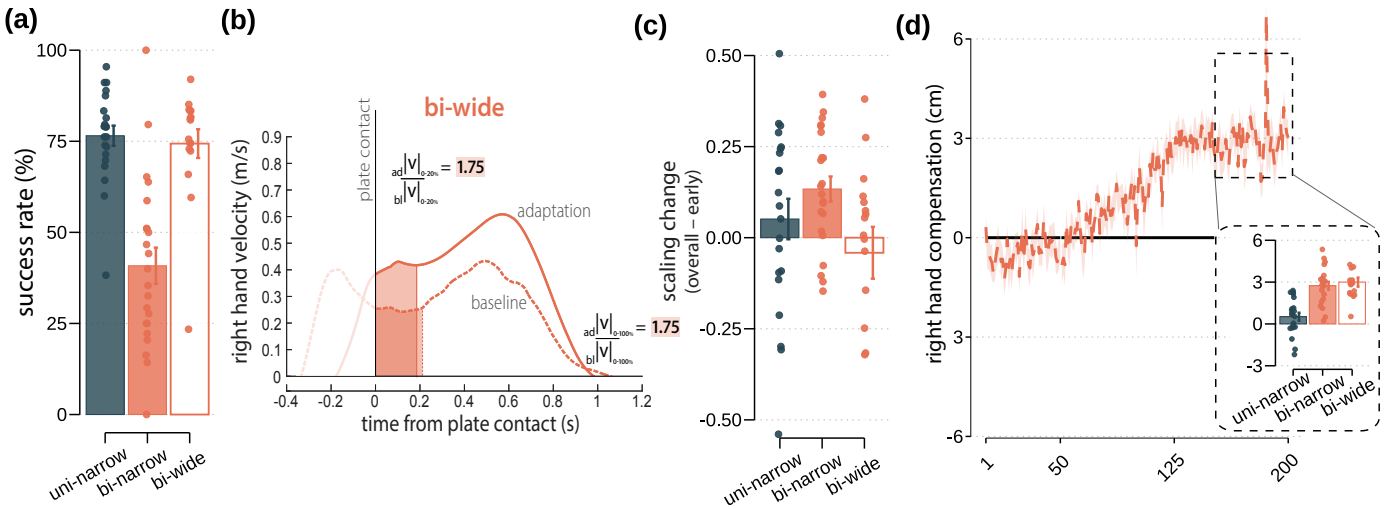
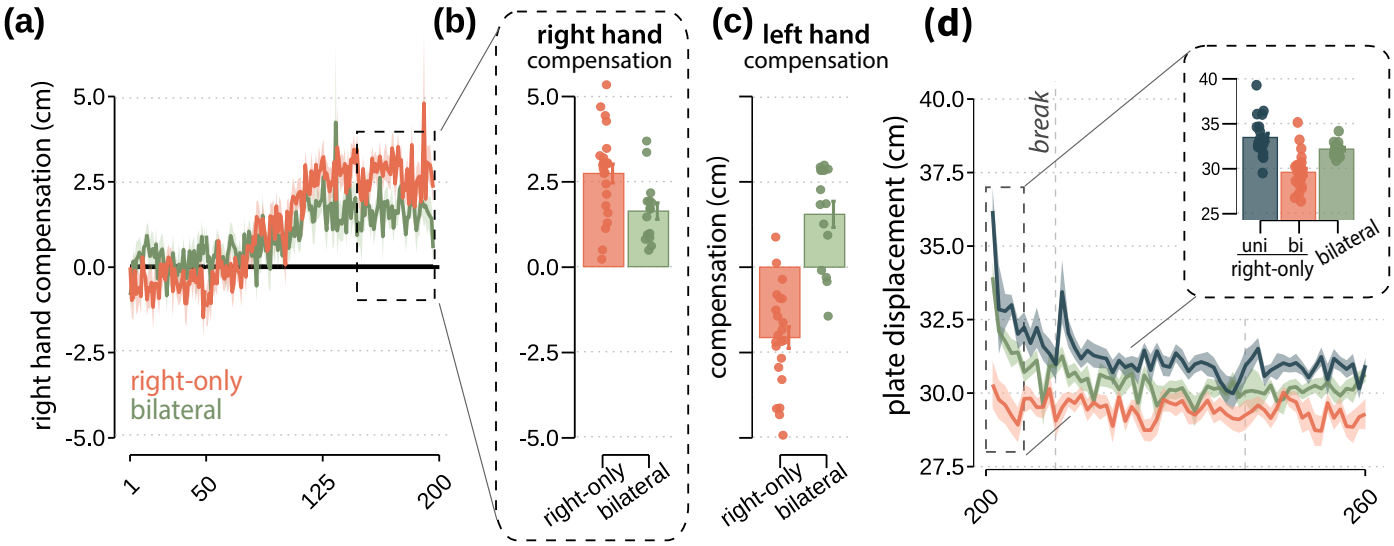
Figure 7. Bilateral gain perturbation reduced hand compensations and restored plate aftereffects. **(a)** Trial-by-trial group averages for right hand compensation showing progressive increase over the adaptation phase in both groups. **(b)** Epoch average for right hand compensation at the end of adaptation showing smaller compensation in the bilateral compared to right-only group. **(c)** Epoch average for left hand compensation at the end of adaptation showing opposite directions of compensation between groups: in the right-only group, the left hand compensated in the opposite direction to the right hand (negative values), while in the bilateral group, both hands compensated in the same direction (positive values). **(d)** Trial-by-trial averages for plate displacement during washout showing aftereffects in all groups. Inset shows epoch average at the start of washout with plate aftereffects in the bilateral group restored toward unimanual levels compared to the right-only group. Error bars/shading represent SEM.