Adaptive learning of a naturalistic bimanual task in virtual reality

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Abstract

Traditional motor adaptation studies often use constrained tasks that limit natural movement strategies. Using virtual reality, we studied people performing a realistic bimanual plate-lifting task while learning to account for a visual gain distortion applied to the right hand. We measured adaptation of early hand speed and the final plate position in three task conditions: bimanual lifting to a narrow target, unimanual lifting to a narrow target, and bimanual lifting to a wide target. As in previous studies, both hands initially adjusted to the distortion in bimanual conditions. But ultimately only the right hand adapted its speed and showed after-effects, contrasting prior reports. Contrary to our expectation, participants did not adapt early speed more when using one versus two hands. When we widened the target zone, participants achieved greater success in final plate position without reducing adaptation of early speed. Finally, both bimanual groups used a strategy of tilting the plate to be successful and showed no after-effects in final plate position when the distortion was removed. In contrast, the unimanual group did not tilt the plate and did show after-effects in final plate position. These findings reveal that in naturalistic tasks, people leverage multiple movement strategies to achieve goals. Overall, our findings support established principles of adaptation but also challenge expectations derived from more constrained motor learning paradigms, highlighting the importance of studying motor learning in more naturalistic contexts.

Significance Statement

Motor adaptation is a key mechanism through which the nervous system maintains and recalibrates movement in changing environments. While this process has potential applications in rehabilitation, most studies rely on simplified tasks that may not reflect real-world motor control. Here, we investigated adaptation in a naturalistic 3D bimanual task using immersive virtual reality. Our findings demonstrate hallmark features of adaptation in this unconstrained environment but also uncover intelligent strategies that exploit redundancy and feedback to achieve task success. By extending adaptation principles to complex, unconstrained movements, this study provides insight into how the nervous system implements learning in unconstrained situations and contributes to the growing effort to make motor learning research more applicable to real-world rehabilitation settings.

Introduction

Despite significant advances in human sensorimotor neuroscience, a critical gap remains between traditional laboratory motor control and motor learning research and its application in clinical rehabilitation and real-world contexts (Bastian, 2008; Roemmich and Bastian, 2018; Leech et al., 2022). Consider the well-studied phenomenon of adaptation. Adaptation is an error-driven process of motor learning driven by a discrepancy between the predicted and actual sensory consequence of the movement (Bastian, 2008). Adaptation has many potential applications for rehabilitation, and it may be a critical mechanism for relearning normative movement patterns after injury (Krakauer, 2006; Bastian, 2008). Except for a few notable examples (Patton et al., 2006; Scheidt and Stoeckmann, 2007; Patton et al., 2013; Abdollahi et al., 2014; Reisman et al., 2007, 2009), the integration of adaptation-based training in motor rehabilitation is somewhat limited.

One reason for this disconnect is that much of what we know about adaptation comes from laboratory tasks designed to control for specific biomechanical demands or isolate specific learning processes (Wolpert et al., 2011). A way to bridge the gap between controlled laboratory research and real-world applications is to understand motor learning in the rich, dynamic environments in which humans move (Ingram and Wolpert, 2011; Mohr et al., 2023). This presents some methodological challenges, including the ability to precisely manipulate visual feedback in real-world settings. Traditional methods like prisms are extremely useful in certain situations but offer less control and flexibility. Virtual reality (VR) provides an alternative to create compelling perceptual illusions via real-time, precise visual manipulations, and has emerged as a valuable tool in behavioral neuroscience (Tarr and Warren, 2002; Bohil et al., 2011), motor learning (Levac and Sveistrup, 2014; Levac et al., 2019) and rehabilitation research (reviewed in Sveistrup, 2004; Adamovich et al., 2009; Levin et al., 2015).

Here, we used a fully immersive, embodied, and controller-free VR game to study adaptation in realistic movement contexts (for detailed description and comparison to previously published VR tasks, see Rossi et al., 2025). This game simulates a shared bimanual task where participants lift a plate of grapes

with both hands to feed birds. The virtual interactions inside the game replicates more natural environments: 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. As players lift the plate of grapes, they need to continuously adjust to the dynamics of their own movements while also responding to unexpected changes in perceived stability, e.g., a perceived unevenness in load when the grapes shift to one side or a sudden feeling of unloading if the grapes slide off the plate.

We first examined how participants adapted to a right-hand gain perturbation in a bimanual lifting task, where maintaining a level plate could be achieved by adjusting right hand alone or both hands. Adaptation is assessed early in the movement, prior to feedback based adjustments in the movement. Based on previous studies (Diedrichsen, 2007; Mutha and Sainburg, 2009; White and Diedrichsen, 2010; Dimitriou et al., 2012; White and Diedrichsen, 2013; Reichenbach et al., 2013; Omrani et al., 2013; Varghese et al., 2023; Kitchen et al., 2023; Diedrichsen and Gush, 2009) we expected both hands to adapt, with the right hand speeding up and the left slowing down, and both showing after-effects. Next, we asked if unimanual adaptation was more robust than bimanual adaptation. We predicted greater adaptation and larger after-effects in the unimanual context since there could be no ambiguity about the right hand as the source of slowing. Finally, we tested if increasing target tolerance affected task success and adaptation (note that task success is also influenced by feedback control). While increasing target size generally improves success, its effect on adaptation is unclear, with some studies suggesting that success enhances adaptation (Nikooyan and Ahmed, 2015) and after-effects (Galea et al., 2015; Reichenthal et al., 2016), whereas others do not (Leow et al., 2018; H. E. Kim et al., 2019). We predicted that a larger target tolerance would reduce adaptation and after-effects because people could take more advantage of the redundancy between hands to solve the task.

Materials and Methods

Participants

Fifty-nine neurotypical volunteers were recruited sequentially into three groups, with each group completing a different version of the adaptation task at a different time (bimanual-narrow: n = 22; unimanual-narrow: n = 21; bimanual-wide: n = 16). Study procedures were approved by the Johns Hopkins Medical Institutional Review Board and all volunteers provided informed consent before participating and were compensated for their time. All participants reported being right-handed. Except for one, all participants were naïve to the paradigm and participated in only one of the three groups.

Experimental Task and Paradigm

Data were collected using the open-source *MovementVR* software platform and detailed description of the task and capabilities of this platform can be found in Rossi et al (Rossi et al., 2025). An updated software with customizable parameters can be found here: https://movementvr.github.io/. The three versions of the game (bimanual-narrow, unimanual-narrow, and bimanual-wide) used in this study can be found here: https://osf.io/8wbkh/ as PC executable applications.

Participants performed a bimanual lifting task in an immersive virtual reality (VR) environment, where they lifted a virtual plate of grapes with both hands transporting it to a target perch at eye level (Figure 1A). The goal was to keep the plate level and reach the target zone accurately without spilling the grapes. The task was implemented using a VR headset (Meta Quest 2) with real-time hand tracking via a LEAP Motion controller (Ultraleap, 2021), allowing naturalistic interactions within the virtual scene. The game environment, developed in Unity, featured physics-based interactions to ensure realistic plate dynamics.

The target perch was surrounded by an orange target zone (Figure 1B), requiring precise placement of the plate. Object sizes and other task-relevant parameters are shown in Figure 1C. In the bimanual-narrow condition, the target zone height was 3 cm, demanding higher precision, whereas in the

bimanual-wide condition, the target zone was 6 cm, allowing for more end-point variability. The plate diameter was 26 cm in the bimanual task and 13 cm in the unimanual version to ensure stable control during transport. Before the experiment, participants watched a video demonstration and completed 20–30 familiarization trials.

The experiment consisted of 260 trials across three phases (Figure 1D). During baseline (50 trials), virtual hand movements matched real-world movements. In the adaptation phase (150 trials), the vertical visual gain of the right hand was gradually reduced (Kagerer et al., 1997; Wong and Shelhamer, 2011) from 100% to 65% over 75 trials (Figure 1D, green line) and then held constant for another 75 trials. Gain perturbations were applied at plate contact to ensure consistent manipulation as the wrist position changed. A final washout phase (60 trials) restored equal visual gains to examine after-effects.

Participants received binary audiovisual feedback upon reaching the target zone. Trials were self-paced but terminated after 30 seconds. Rest breaks were provided every 30 trials (Figure 1D, vertical dashed lines) to minimize fatigue without coinciding with experimental transitions. Participants did not take off the headset during breaks. 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’?”).

Kinematic data processing and analysis

Postprocessing was done in MATLAB 2021b (MathWorks Inc.). Movement onset and offset were detected automatically in Unity and verified manually. Movement onset was defined as the first frame of plate movement, and offset was determined by the earliest frame when the right hand or plate reached the highest vertical position. Trials with less than 50% plate displacement were excluded from further analysis.

Adapting to gain perturbations requires learning a new scaling factor that maps one's motor commands (input) to the movement extent (output) (Gordon and Ghez, 1987a, 1987b; Krakauer et al., 2000). To track learning to the gain perturbations, we developed three key measures: 1) early speed scaling, 2) displacement scaling, and 3) success rates.

Early speed scaling captured the adaptive feedforward component of learning, calculated as the average hand speed at 20% of total vertical displacement. We quantified right-hand speed relative to baseline and relative to the left hand. We selected a 20% spatial landmark to mitigate sampling irregularities with Unity and accommodate small inter-individual variations in total displacement.

Displacement scaling assessed total feedforward and feedback-based adjustments by measuring the displacement of plate center and wrist positions from movement onset to offset. Six displacement measures were analyzed: plate displacement, 'seen' and 'real' right wrist displacement, left wrist displacement, tilt contribution, and total displacement.

All scaling measures, including for early speed and displacement, were normalized to each participant's baseline epoch (last 10 trials), producing a scaling factor. To fully compensate for the perturbation, where the seen right hand moves 65% of the 'real' right hand, the 'real' right hand would need to scale 1.538 times above baseline by the end of the adaptation phase.

Success rates were calculated based on the binary reward outcomes of trials within experimental epochs defined as follows: baseline (last 10 trials), ramp phase (first and last 25 trials), plateau phase (first and last 25 trials), and washout phase (first 5 and last 10 trials). Average values for scaling measures, including for early speed and displacement, were also calculated for these epochs.

Statistical analysis

Statistical analyses were conducted in R (version 4.4.1).

We fit linear mixed-effects models to trial-level data in the pre-defined epochs with random intercepts for participants to account for individual variability. Outcome variables included R/L speed and displacement scaling ratio, right-hand speed and displacement scaling, and left-hand speed and displacement scaling. As we did not intend to compare data between the hands, we ran separate models for the left and right hands, as well as for R/L scaling ratio.

In the bimanual-narrow group, to test how people adapted to the gain perturbation, we included a fixed offset of 1. The fixed offset of 1 allowed us to shift the intercept to 1 so that all comparisons were to 1 instead of the default value of 0. The model was of the following form:

$$\text{Model 1: } \mathrm{outcome} \sim 1 + \mathrm{offset}(1) + \mathrm{epoch} + (1|\mathrm{subj})$$

Then, to compare speed and displacement scaling measures between groups across epochs, we added '*group'* as a separate fixed and interacting effect to the above model:

$$\text{Model 2: } \mathrm{outcome} \sim 1 + \mathrm{epoch} + \mathrm{group} + \mathrm{epoch} \times \mathrm{group} + (1|\mathrm{subj})$$

…where independent variables *group* and *subj* were nominal categorical variables, *epoch* was an ordinal categorical variable.

Specifically, the '*epoch*' factor in both models had 7 levels, corresponding to the experimental epochs described above, with the baseline epoch as the reference level. Model 2 was run for two separate comparisons: (a) between bimanual-narrow and unimanual-narrow and (b) between bimanual-narrow and bimanual-wide, with the bimanual-narrow group as the reference level in both comparisons. Thus, the '*group*' factor had two levels for each comparison. We did not have any a-priori hypotheses about comparisons between unimanual-narrow and bimanual-wide groups. Lastly, to compare success rates, we used a simple linear model across the three groups.

For significant effects in the mixed models, post-hoc comparisons of estimated marginal means were conducted using the '*emmeans'* package in R, with Bonferroni adjustments for multiple comparisons

(Lenth, 2021). For Model 1, after confirming that baseline intercept was not significantly different from 1, we compared the baseline epoch with adaptation and washout epochs. For Model 2, we evaluated the interaction '*group* x *epoch*' using a difference-in-difference analysis. Specifically comparing the change in the outcomes from baseline to adaptation and washout epochs between: (a) the bimanual-narrow and the unimanual-narrow group, and (b) the bimanual-narrow and the bimanual-wide group. Assumptions for generalized linear models were checked and robust models (Koller, 2016; Greco et al., 2019) were chosen for the individual hand scaling outcomes. We repeated the analysis with and without the one participant who was not naïve and did both experiments and confirmed the estimates of the model.

Results

People adapted by increasing the early speed of the right-hand.

Participants in the bimanual-narrow group adapted to the gain perturbation by speeding up their right hand relative to their left hand (i.e., R/L scaling ratio, end plateau: 1.20 ± 0.01, $p<0.001$; Figure 2A & B). Early R/L scaling accounted for 78% of the total size of the perturbation (i.e., 1.538). As expected, R/L scaling ratio showed significant after-effects (start washout: 1.15 ± 0.02, $p<0.001$). Interestingly, we found that the individual behavior of each hand and the contribution to the scaling ratio changed across the learning block. Participants initially compensated for the perturbation by scaling down (slowing) their left hand (Figure 2C & D, end ramp: 0.92 ± 0.02, $p=0.004$), as opposed to scaling up (speeding) their right hand (diff from baseline, end ramp: 0.04 ± 0.02, $p=0.6$). But by the end of learning phase, the scaling ratio was driven primarily by the right hand scaling up (end plateau: 0.20 ± 0.02, $p<0.001$) while left hand scaling returned to baseline (end plateau: 0.002 ± 0.02, $p=0.99$; Figure 2C & D). When looking at hand-specific scaling effects, only the right-hand scaling showed significant positive after-effects (start washout: 0.11 ± 0.04, $p=0.01$). The left-hand scaling does not show significant after-effects (start washout: 0.05 ± 0.03, $p=0.95$; Figure 2C & D). Thus, although the initial response to right-hand perturbations is distributed between hands, over time, participants compensate for errors and retained after-effects with the right hand only.

Early speed of the right-hand increased during adaptation in bimanual and unimanual contexts.

To understand if the right-hand adaptation is lessened in the bimanual context, we compared performance of the bimanual-narrow group with a second group (n = 21) that learned right hand gain perturbations in the unimanual context.

Compared to baseline, there was no significant difference in right hand scaling between the two groups at the end of the learning block (end plateau: diff = 0.07 ± 0.05, $p=0.63$) or the start of washout (0.07 ± 0.04, $p=0.45$; Figure 3 A & B). Initially, participants demonstrated slightly larger right hand early speed adaptation in the unimanual group compared to the bimanual group, but this effect was not statistically

significant (end ramp: 0.08 ± 0.04, unadj. p=0.048, adj. p=0.29). Interestingly, speed scaling effects persisted into the end of washout in the unimanual group and were significantly larger than the bimanual group (end washout: 0.19 ± 0.04, p<0.001; Figure 3C) suggesting a potential benefit of continued unimanual practice. Thus, experiencing right hand errors in the bimanual context did not reduce its overall magnitude of adaptation or after-effects.

The bimanual-narrow group had less success than unimanual-narrow group but performed equally when the target was widened.

During the learning block, success rate decreased in all three groups (epoch effect: F (6,392) = 24.14, p<0.001) with an average decrease of 21.4% by the end of learning (end plateau) and 29.2% at the start of the washout phase but returning to baseline level by the end of the washout phase (avg. diff. from baseline of 0.37%). The pattern of decrease was similar across the groups (epoch x group effect: F (12,392) = 1.08, p=0.377) and mirrored the perturbation.

Although target size was the same, success rate was significantly lower in the bimanual-narrow group compared to the unimanual-narrow group across epochs (Figure 4; 29.9 ± 2.2%, p<0.001). When accuracy demands were eased in the bimanual-wide group, success rates were significantly higher compared to the bimanual-narrow group (averaged difference across epochs: 30.4 ± 2.3%, p<0.001) and were comparable to the unimanual-narrow group (avg diff: 0.52 ± 2.4%, p=0.973). Thus, we could successfully modify success rates by increasing target tolerance in the bimanual context.

Widening the target also led to larger after-effects in early speed scaling.

Compared to the bimanual-narrow group, the bimanual-wide group showed a trend towards larger relative speed scaling between hands (R/L scaling ratio) at the end of adaptation (end plateau: diff = 0.04 ± 0.02, unadj. p=0.026, adj. p=0.15). Contrary to our expectation, the bimanual-wide group also showed larger after-effects at the start of washout (0.08 ± 0.02, p=0.004; Figure 5A & B).

Similar to what was seen in the bimanual-narrow group, the scaling ratio in the bimanual-wide group was primarily driven by the right-hand speeding up. The bimanual-wide group showed larger scaling of right-hand speed initially (end ramp: diff = 0.24 ± 0.04, $p<0.001$). But, by the end of the learning phase, both groups showed similar right hand speed scaling (0.05 ± 0.04, $p=0.99$). After-effects in right hand speed scaling were also similar between the groups (0.005 ± 0.06, $p=0.99$; Figure 5C & D).

Interestingly, left hand contribution to the scaling ratio showed a different pattern between the bimanual-narrow and bimanual-wide groups. In the bimanual-wide group, people initially scaled up left-hand early speed, rather than scaling down as in the bimanual-narrow group (end ramp: diff from baseline = 0.20 ± 0.04, $p<0.001$). By the end of learning, left-hand speed was near baseline level and there was no difference between the groups (end plateau: diff = 0.03 ± 0.04, $p=0.99$). Consistent with the narrow-target group, there were no after-effects in left hand speed scaling in the wide-target group (start washout: diff = 0.02 ± 0.05, $p=0.99$; Figure 5E & F). Interestingly, although scaling ratio at the end of washout was back to baseline level (end washout: diff = 0.03 ± 0.02, $p=0.99$), individual hand scaling continued to increase (end washout: right hand diff = 0.21 ± 0.05, $p<0.001$; left hand diff = 0.18 ± 0.04, $p<0.001$), likely due to improved speed-accuracy tradeoffs from continued practice.

Taken together, increasing target tolerance boosted success (Figure 4) and led to larger initial scaling in both hands and larger after-effects in the early scaling ratio between hands but did not reduce the overall magnitude of adaptation or after-effects in the right hand. It is important to note that success or failure did not depend on early speed scaling but rather depended on the final position of the plate. This is why in the washout phase early speed scaling could be maintained (after-effects) while still being successful if participants engaged feedback-based corrections to rapidly slow down and stop at the target. The contributions of feedback-based corrections and other compensatory strategies to achieve the final position of the plate and hands will be examined next.

How do people successfully move the plate into the target zone?

In this section, we examine the final position of the plate and the distance traveled by the hands to appreciate the combined contributions of feedforward, feedback and other compensations made throughout the entire movement trajectory to achieve success.

We first consider the final position of the plate, which closely maps to success or failure. Figure 6D shows an individual example of this measure plotted trial by trial for the bimanual narrow group. Note that there is no after-effect in this example, due to the use of feedback control and compensations. Figures 7A and B show group data, where the bimanual groups move farther into the target at the end of adaptation (end plateau, diff. = 0.04 ± 0.01, $p<0.001$), but only the unimanual group showed after-effects (start washout, diff = 0.08 ± 0.01, $p<0.001$). This was due to the unimanual group relying more on feedforward control to reach the full distance. The two bimanual groups used feedback control and compensation to reach the full distance and achieve success.

What were the compensations used by the bimanual groups? Figure 6 describes several measurements that explain this phenomenon. Interestingly, at the end of adaptation, the 'seen' and the 'real' right hand moved less than expected to counteract the gain perturbation. Figure 6E and H show these measures in an individual example from the bimanual narrow group. Figure 7C and D show group data, where the bimanual groups moved their right hand less than the unimanual group at the end of adaptation (end plateau, 'seen' hand diff. = 0.08 ± 0.02, $p<0.001$; Fig 7F–I), and the unimanual group showed larger after-effects (start washout, 'seen' hand diff. = 0.04 ± 0.01, $p=0.017$).

How then did the bimanual groups accomplish the final plate position to achieve success? Despite moving their right hands less, participants in the bimanual groups were able to achieve success by tilting the plate up. As pictured in Figure 6C, a tilt might involve flexing the right wrist and moving the plate up with the fingers (i.e., balancing a level plate on the tips of the fingers). A tilt could also occur because the left hand is slightly higher than the right positioning the plate's center at the target as in the

example in Figure 6F. Thus, tilting made it so that the plate center reached the target even when the right hand did not.

We quantified the difference between the ‘seen’ right hand and the plate center as a proxy for an added strategy—a tilt (Fig 6G). At the end of adaptation, the tilt compensation was only observed in the bimanual groups (end plateau, diff. = 0.09 ± 0.01, $p<0.001$) and allowed these groups to achieve similar total displacement as the unimanual group (0.02 ± 0.01, $p=0.09$). After-effects in tilt compensations in the bimanual groups were in the opposite direction (start washout, diff = 0.04 ± 0.01, $p=0.002$) and so led to smaller after-effects in total displacement compared to the unimanual group (0.08 ± 0.01, $p<0.001$). Together, these results suggest that tilt contributions are intelligent compensatory strategies that the nervous system employs to take advantage of redundancies at the wrist and hand in this unconstrained task.

Discussion

In this study, we investigated a gain adaptation in an unconstrained naturalistic task using a novel virtual reality paradigm. By simulating a shared bimanual task where both hands lifted a virtual plate, we demonstrate that people can effectively adapt to visuomotor gain perturbations of the right hand. The visual gain perturbation caused the 'seen' (virtual) right hand to appear to move less than the 'real' right hand, creating an illusion of 'slowing.' People learned to respond to this slowing in a feedforward manner by speeding up the right hand relative to the left hand (scaling ratio) early in the movement and retained this movement scaling pattern when the perturbation was removed (after-effects). Learning in the right hand itself was relatively robust to alterations in contextual features such as moving unimanually or when target tolerance was increased (bimanual-wide). That is, the magnitude of adaptation and after-effects in right hand early speed scaling was not different between the bimanual-narrow compared to unimanual-narrow or bimanual-wide groups.

We did however find some unique differences in the (non-perturbed) left-hand response in the two bimanual conditions. Similar to previous studies (White and Diedrichsen, 2010; Omrani et al., 2013; Varghese et al., 2023), we found that during the learning phase both hands produced coordinated responses to the right hand's gain perturbation. Notably, participants in the bimanual-narrow group adapted to gain perturbations in the right hand by increasing early speed scaling and initially showed compensatory slowing of the unperturbed left hand. But by the end of practice and at the start of the washout phase, the adapted interlimb response was primarily driven by the right hand while the left hand did not show significant after-effects.

The absence of left-hand after-effects suggests its initial response was compensatory. This contrasts with some prior work on planar bimanual reaching (Diedrichsen, 2007). Diedrichsen et al. showed that when one hand was perturbed by a force field, both hands adapted and showed after-effects. A key difference between that study and ours is in how the shared object was represented. A cursor representation could have increased the ambiguity between the hands allowing both hands to adapt to

the cursor's error. Whereas in our task, the tilt of the virtual plate provides an additional cue to right-hand errors reducing the redundancy between hands. Thus, additional sensory cues in naturalistic tasks, particularly visual cues like plate tilt in the VR environment, may facilitate more precise error assignment compared to simplified laboratory tasks.

Furthermore, the compensatory response of the left hand seems flexible. Support for this comes from observing left hand scaling during the initial learning phase in the bimanual-wide group. In both bimanual groups, the left hand moves slower than the right hand (R/L ratio>1), but compared to its own baseline, the left hand shows contrasting responses in the bimanual-narrow and bimanual-wide groups (Fig 5 E & F): it slows down in the bimanual-narrow group but speeds up in the bimanual-wide group. This contrasting response suggests that the left hand's compensation depends on the right hand's current state rather than its own previous state, i.e., the left hand compensates for the right hand's error (i.e., right hand feels slower) rather than a perceived left-hand error (i.e., left hand feels faster).

Similar task-specific flexibility in compensatory response has previously been observed in the unperturbed hand in non-redundant 2D bimanual tasks (Diedrichsen and Gush, 2009). In that study, a force field perturbation was applied to one hand while participants bimanually controlled a 2D bar of flexible length, with differing task goals: aligning the center of the bar in a target (allowing hand distance to vary) or maintaining the bar's length (allowing the center position to vary). When the goal was to maintain bar length, the unperturbed hand moved in the same direction as the perturbed hand; when the goal was to align the bar's center, the unperturbed hand moved in the opposite direction. Similarly, in our task, maintaining an even plate allowed for flexibility, with the left hand adjusting its speed relative to the right hand. In the bimanual-wide group, greater target tolerance enabled faster right-hand speeds, so the left hand scaled appropriately to preserve coordination and achieve the task goal.

Contrary to our expectations, we found that the added challenge of error assignment in the bimanual context did not substantially reduce early speed scaling compared to the unimanual learning. Right-

hand early speed adaptation did not fully decay in the unimanual group, i.e., the right-hand speed scaling was larger in late washout, compared to baseline. Given that this was also observed in the bimanual-wide group in late washout, it might point to a more general performance benefit from practicing in easier conditions (only one hand or larger target) especially when success rate can be maintained through feedback-based corrections.

However, the bimanual context did reduce after-effects in plate center displacement compared to unimanual learning (dark green traces, Figure 7). We interpret this as the unimanual group relying more on feedforward control whereas the two bimanual groups using more feedback control and compensation to reach the full distance and achieve success. This was evident in the emergence of tilt strategies in the bimanual groups where participants tilted the plate to reach the target rather than fully adjusting right-hand height to match the perturbation. It could be that veridical sensory feedback from the left arm in these groups provides stronger cues of the visuo-proprioceptive mismatch between the hands, prompting participants to use tilt compensations to reconcile the discrepancy. Moreover, tilting the right hand conferred no advantage as the plate was centered on the hand, rather tilting would only introduce instability. Interestingly, after-effects in tilt were in the opposite direction which further suggests that the tilt is a compensatory strategy tacked on to achieve movement goals. This unexpected finding highlights how learners leverage additional degrees of freedom in naturalistic tasks to achieve movement goals (Levac and Sveistrup, 2014; Levac et al., 2019), especially when faced with conflicting sensory information.

Our methodological approach using fully embodied virtual reality with real-time hand tracking represents a significant advancement over previous studies that relied on simplified representations or constrained movements. This paradigm maintains experimental control while allowing for natural three-dimensional movements and object interactions, providing a powerful tool for investigating motor learning in conditions that more closely approximate real-world tasks. However, it fails to simulate the proprioceptive and haptic feedback present in real-world tasks. Promising new advances in haptic

feedback-integrated VR systems (McAnally and Wallis, 2022; Nisky and Makin, 2024) will help overcome these challenges.

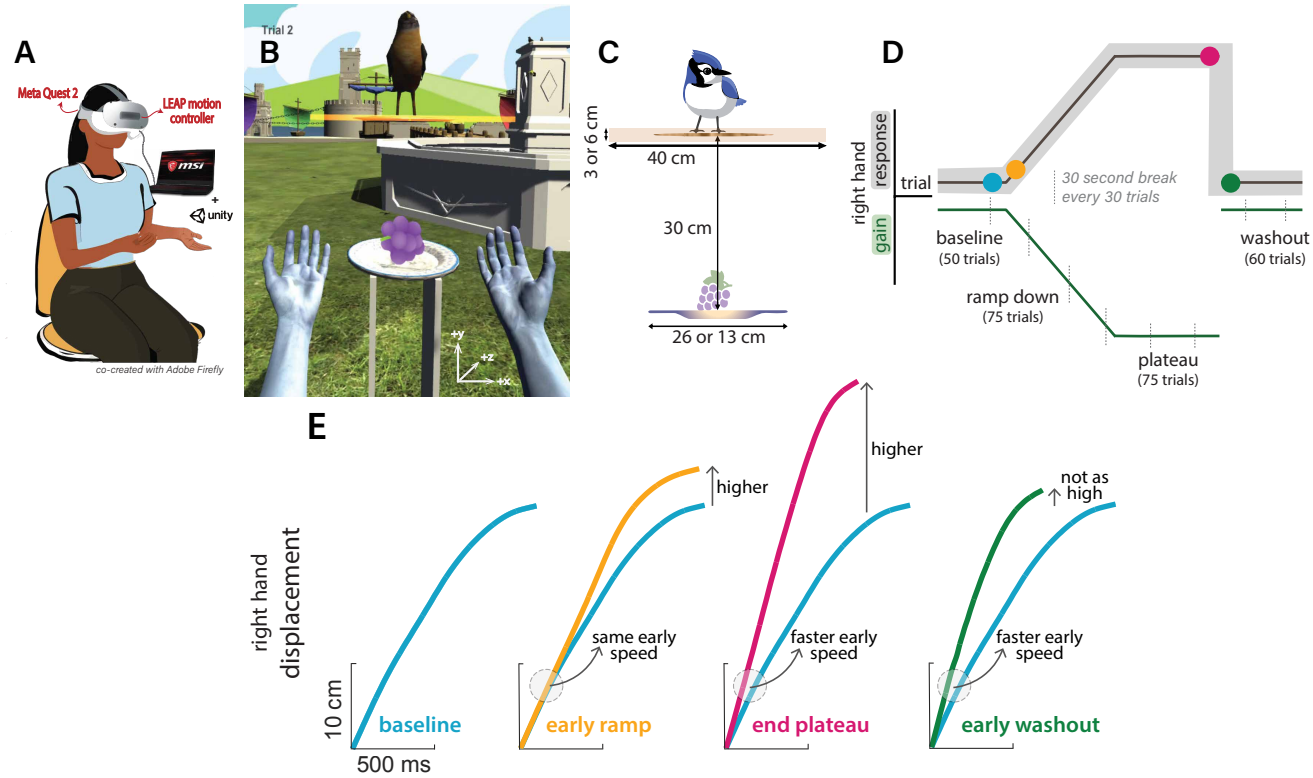
Previous studies indicate that even with fewer virtual elements and simplistic interactions, virtual environments can significantly increase cognitive load and is related to less learning and transfer to the real world (Frederiksen et al., 2020; Buchner et al., 2022; Juliano et al., 2022). In a previous study of adaptation in VR (Juliano et al., 2022), learning via explicit strategy use was related to reduced retention at 24-hours. In the present study, by informally interviewing our participants, we found that none of the participants reported explicit knowledge of the gain perturbation. Instead, they reported feelings of tiredness, especially of the perturbed right hand. Nonetheless, cognitive, specifically visuospatial processing load, is a valid concern and needs further testing in our study.

Gamified movement training with portable, affordable technology like VR can make therapy more engaging and facilitate high-volume practice (Krakauer et al., 2021) in the clinic. More importantly, it may encourage at-home practice to maximize gains (Borstad et al., 2018). Simulating naturalistic adaptation tasks in enriched, less constrained environments may improve skill transfer beyond VR and lead to longer-lasting benefits (Kim et al., 2019). However, key questions remain: How well does VR-based adaptation training transfer to the real world? Can it reduce specific impairments, improve function, or increase participation in clinical populations? Addressing these questions will be crucial for advancing the clinical and real-world application of motor learning in VR.

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

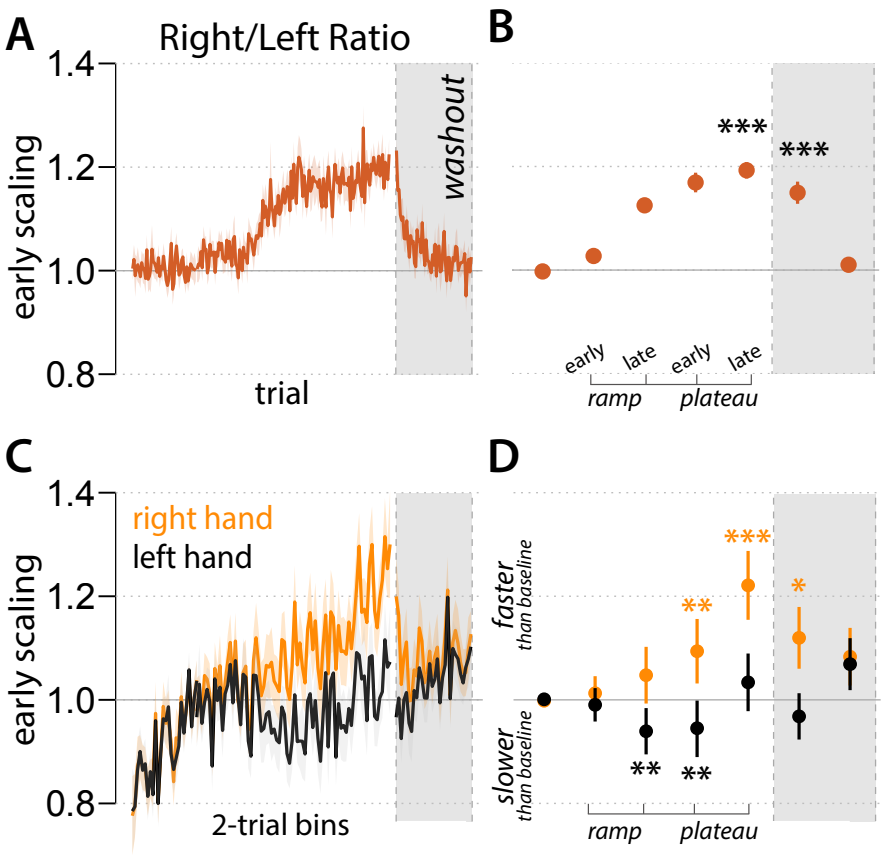
Figure 1



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) Averaged right hand vertical displacement from one participant showing canonical response to the gain perturbation. We calculated early speed defined as the average speed at 20% of the total hand displacement, represented approximately here by the circled area. Note that as perturbation ramps up (yellow), initially right hand moves higher, but its early speed is like it was at baseline (blue). As perturbation size plateaus and towards the end of practice (pink), right hand moves higher and with faster early speeds. During washout (green), right hand continues to move faster reflecting the adapted state even though it may correct online to avoid overshooting (i.e., not reach as high). In this unconstrained naturalistic task, to accommodate people moving at different speeds at baseline, we normalized early speed at the various learning epochs to each person's own baseline early speed to quantify "scaling factor."

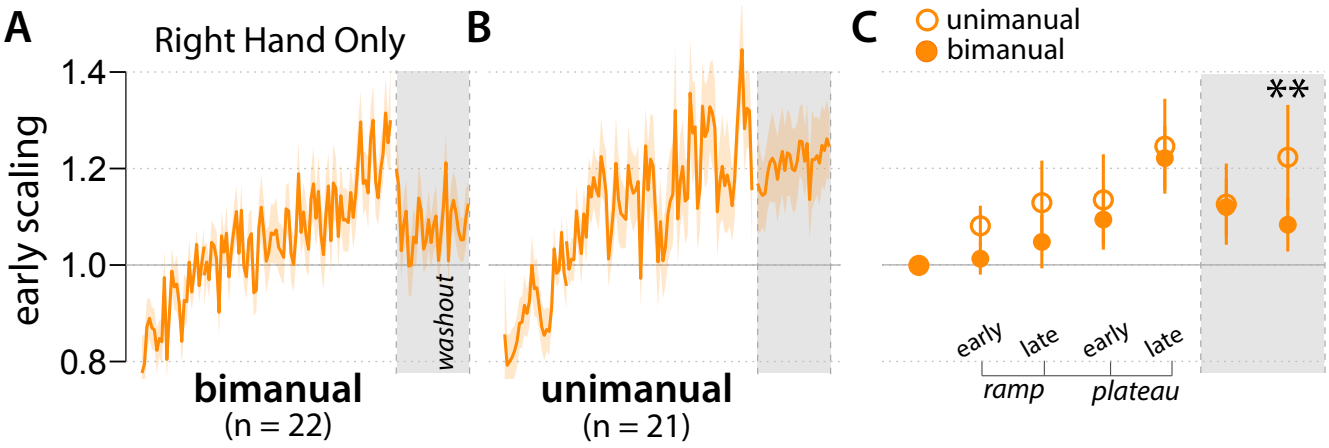
3

Figure 2



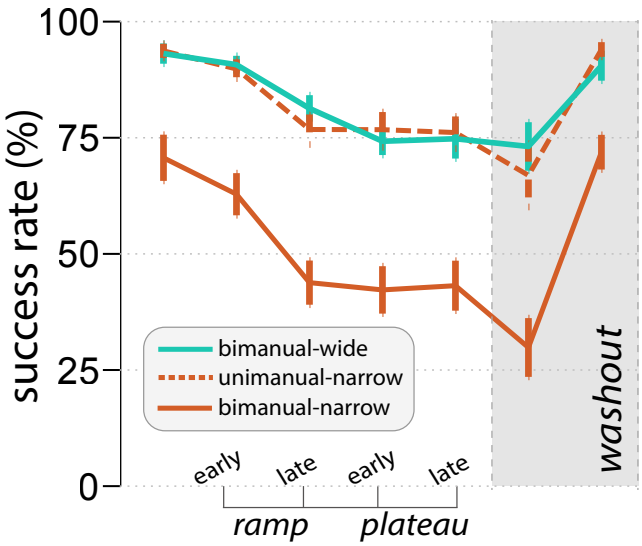
People were able to adapt early scaling of right-hand speed to right-hand perturbations in an unconstrained naturalistic bimanual task. (A) Relative speed scaling between hands; right/left scaling ratio across trials (mean ± se) and (B) by practice epoch. (C) Scaling breakdown by hand across practice binned by every 2 trials (mean ± se) and (D) by practice epochs. The tick marks correspond to the learning phase epochs: the start and end of ramp, and the start and end of plateau. All values are mean ± se. Adjusted *p*-values from post-hoc comparisons of estimated marginal means between baseline and learning and washout epochs: *<0.05, **<0.01, ***<0.001

Figure 3



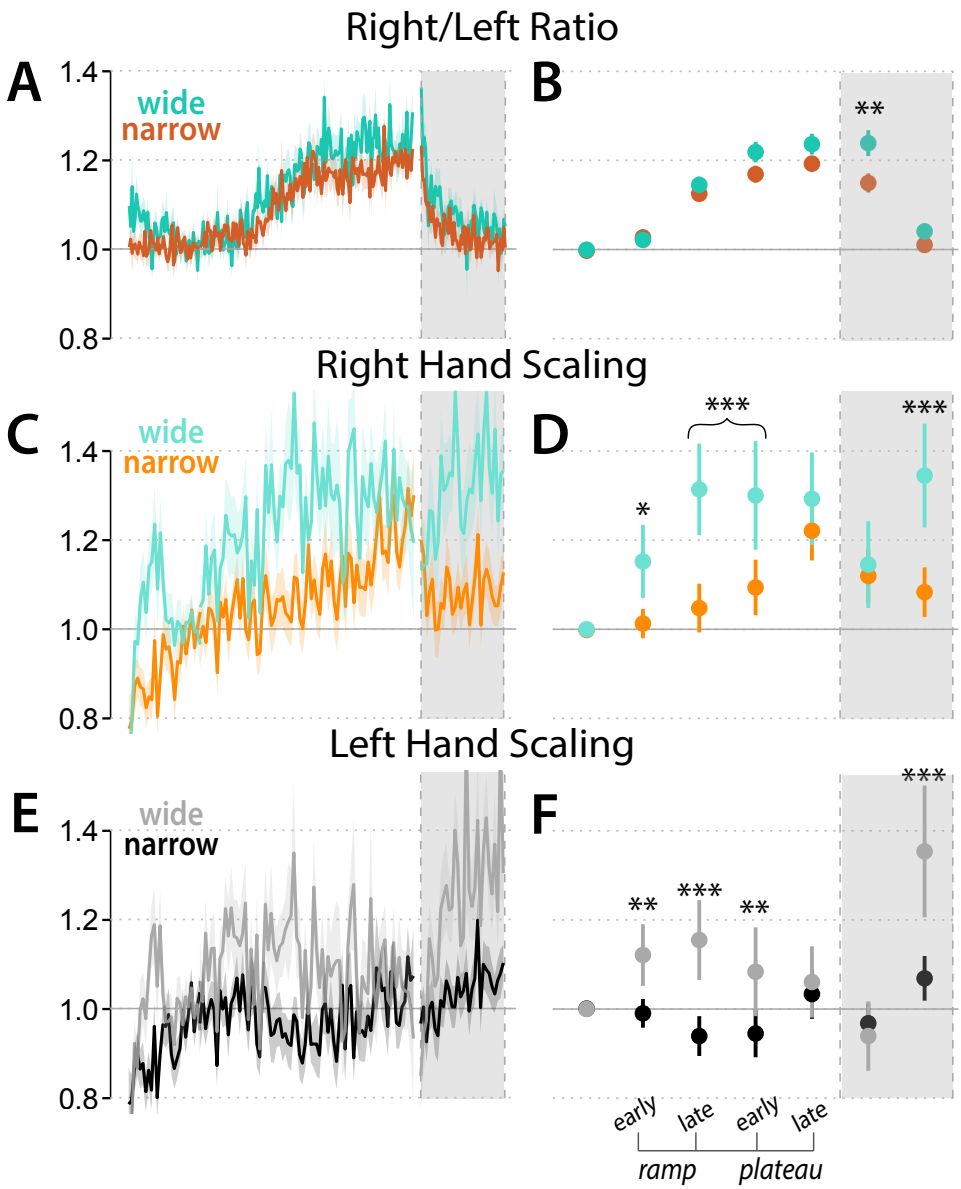
Adaptation of right-hand speed is similar between bimanual and unimanual groups. (A) Averaged right hand speed scaling binned by every 2 trials in the bimanual and (B) unimanual context. (C) Right-hand early speed scaling by practice epochs. The tick marks for four learning epochs correspond to the start and end of ramp, and the start and end of plateau. All values are mean ± se. Adjusted *p*-values from group differences in change from baseline to learning and washout epochs: *<0.05, **<0.01, ***<0.001

Figure 4



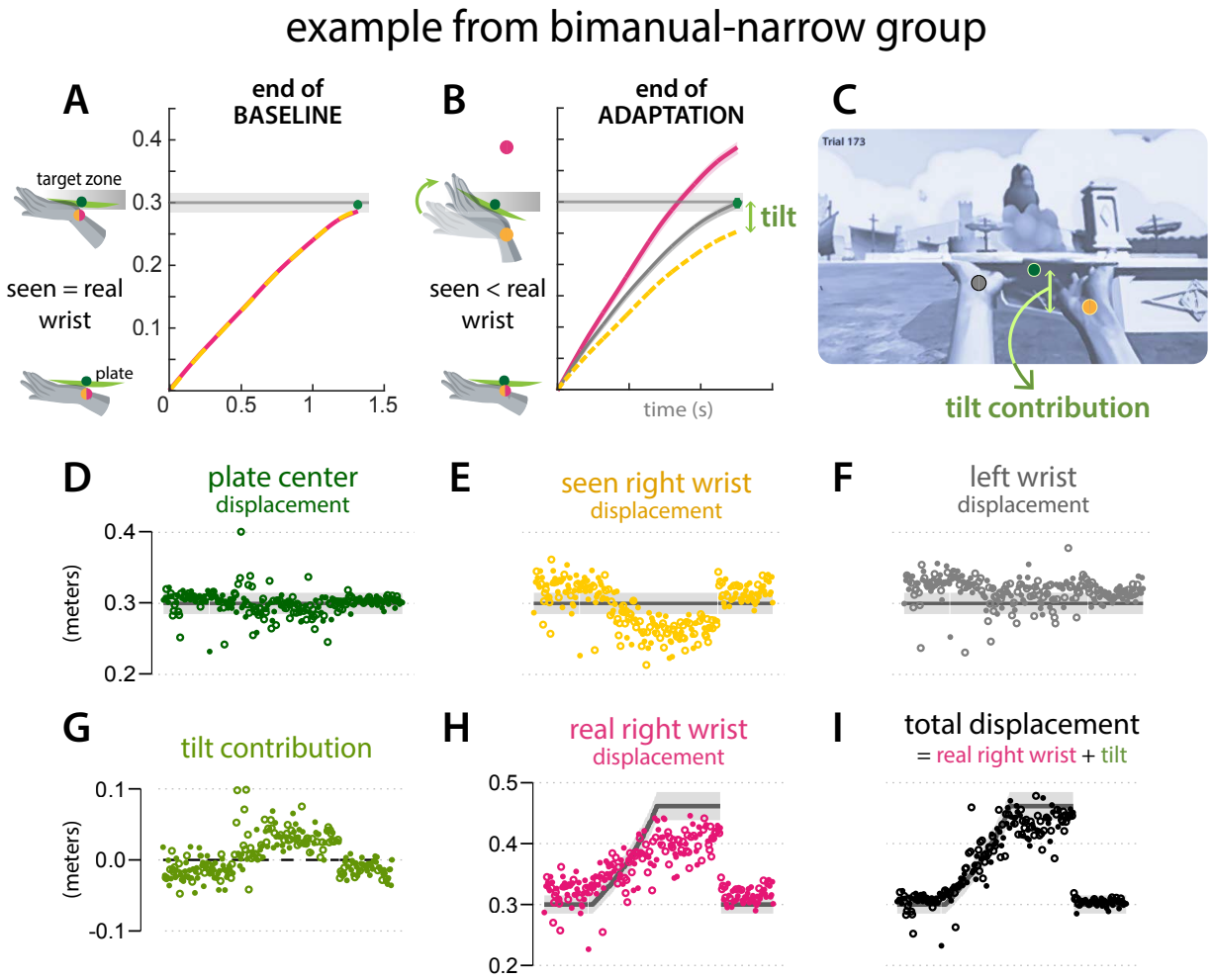
Success rates across practice epochs (mean ± se). All groups fail more during the learning phase and the pattern mirrors the perturbation. Bimanual narrow fails more than the other two groups.

Figure 5



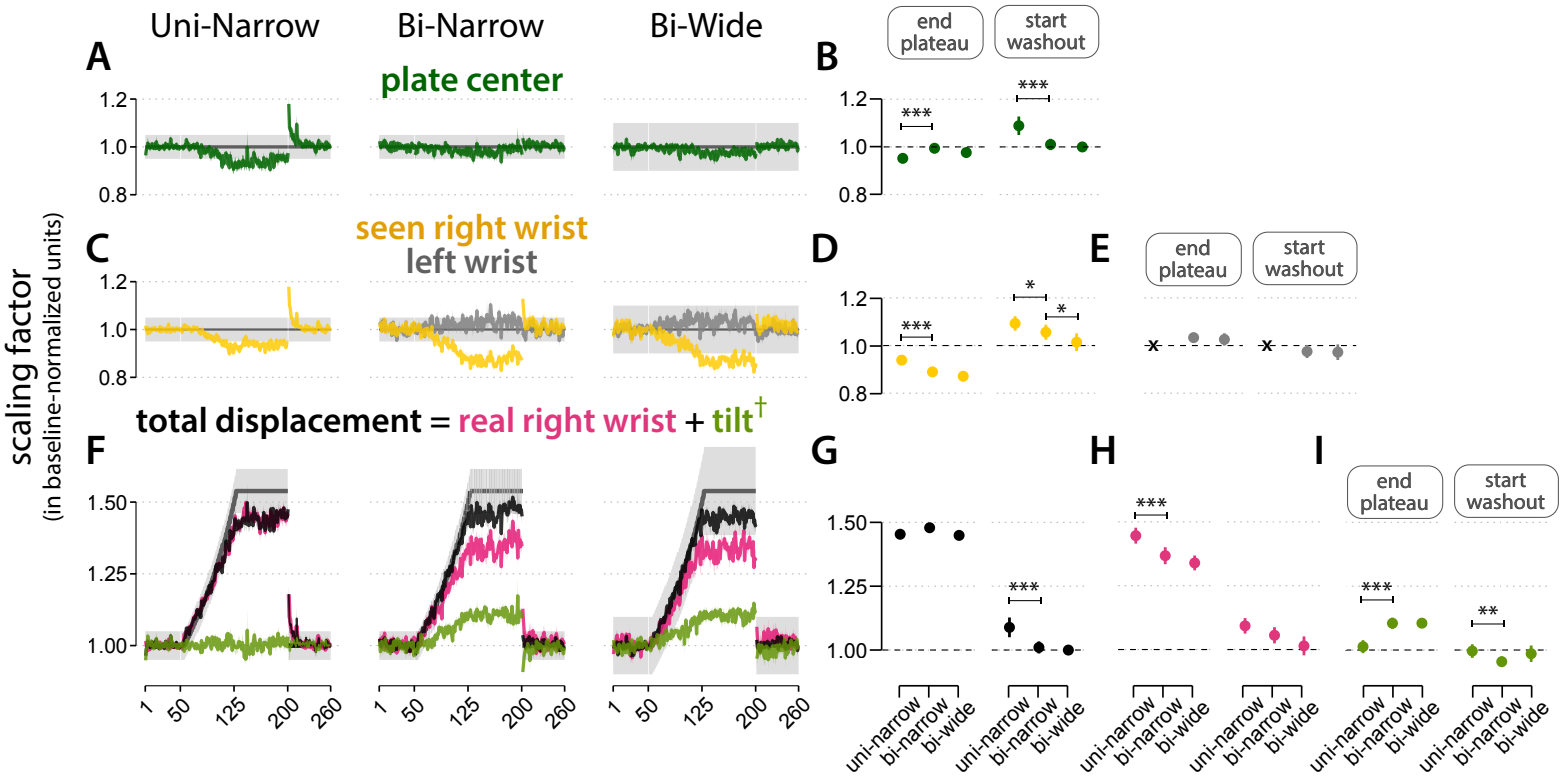
Adaptation of relative scaling between hands improves with wide target, but individual hand scaling is similar between groups. (A) Averaged R/L scaling ratio for the narrow (orange) and wide (teal) groups across trials and (B) by practice epochs. (C) Averaged right hand speed scaling in the two groups binned by every 2 trials and (D) by practice epoch. (E) Averaged left hand speed scaling in the two groups binned by every 2 trials and (F) by practice epoch. The tick marks for four learning epochs correspond to the start and end of ramp, and the start and end of plateau. All values are mean ± se. Adjusted *p*-values from group differences in change from baseline to learning and washout epochs: *<0.05, **<0.01, ***<0.001

Figure 6



Example from one participant in the bimanual group showing that wrist displacement at the end of adaptation is incomplete and a tilt strategy is added. (A) Hand and plate displacement at the end of baseline and (B) at the end of adaptation with illustrations showing tilt contributions added to the right wrist displacement. (C) Coronal game view from a different participant showing similar strategy in real-time game play at approximately the end of single lifting trial. (D) Plate, (E) seen/virtual right wrist, (F) left wrist displacements, as well as (G) tilt contribution computed as (seen right wrist displacement – plate center displacement), (H) real right wrist displacement, and (I) total displacement computed as (real right wrist displacement + tilt). All y-axis units in meters. Open circles are unsuccessful trials while closed circles are successful trials.

Figure 7



Group data showing adaptation strategy differs between bimanual and unimanual groups as people in the bimanual group explore additional degrees of freedom at the hand. (A) Plate displacement (dark green) across trials and (B) averaged by epochs end of plateau and start of washout. (C) Seen hands—left (gray; only for bimanual groups) and right (yellow) across trials and (D & E) averaged by epochs. (F) Real right hand (pink), tilt contribution (bright green; † note that tilt is represented here as (1 + tilt) to allow visualization on same scale as the right hand, and their sum, the total displacement (black) across trials, and (G-I) averaged by epochs. Trial-series data are presented as mean ± se and epoch data are presented as mean ± 95% CI.

3

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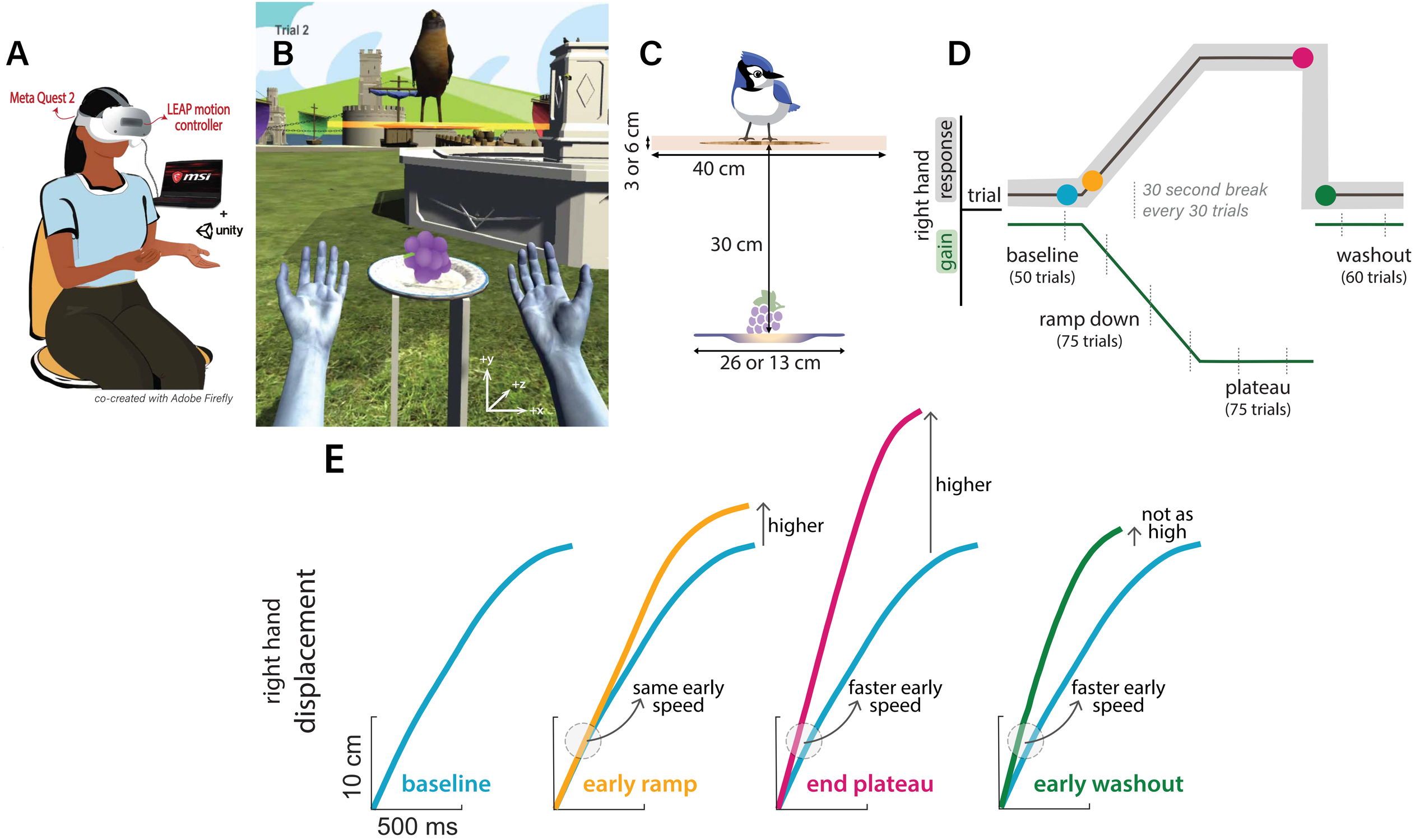
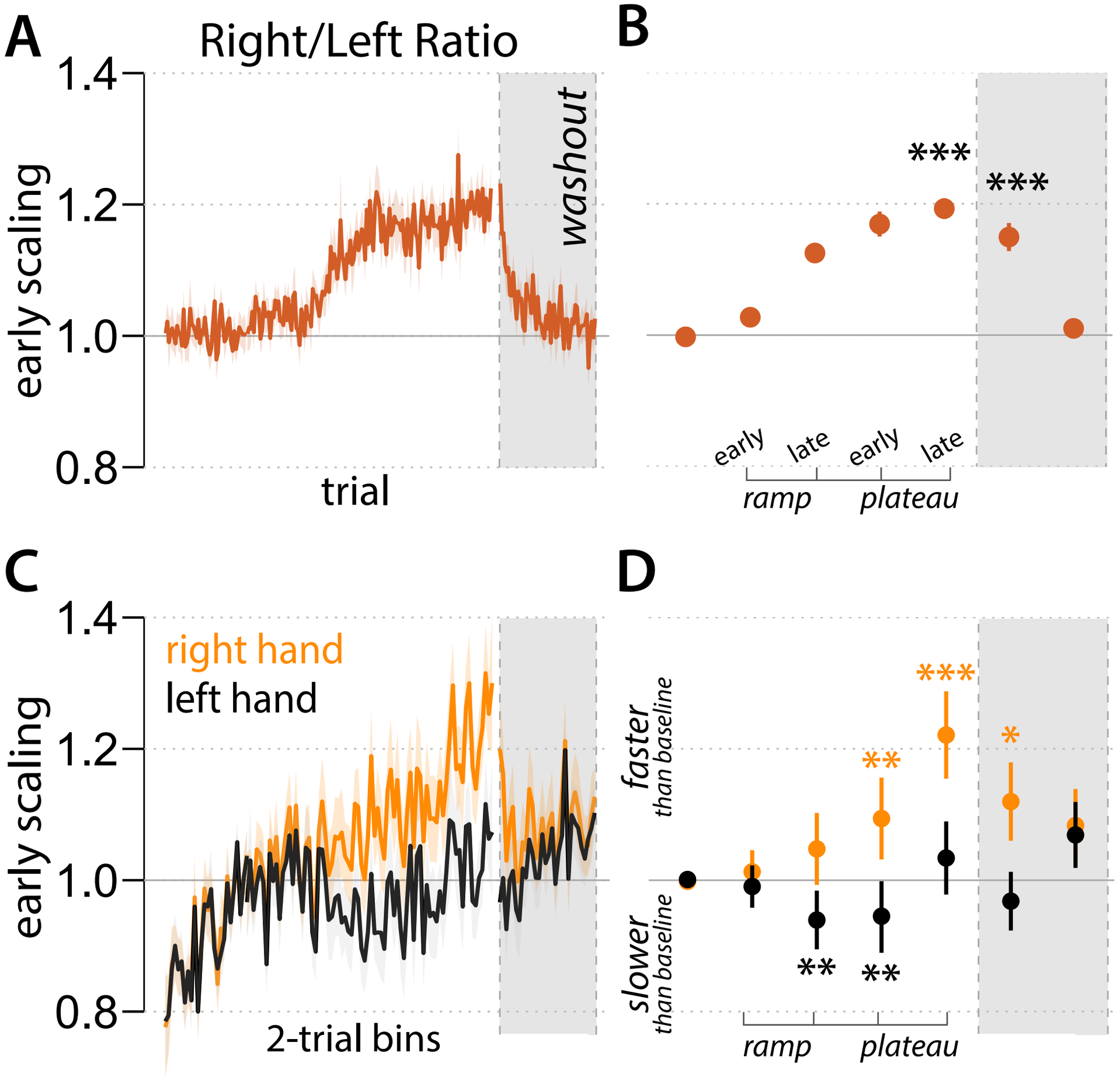
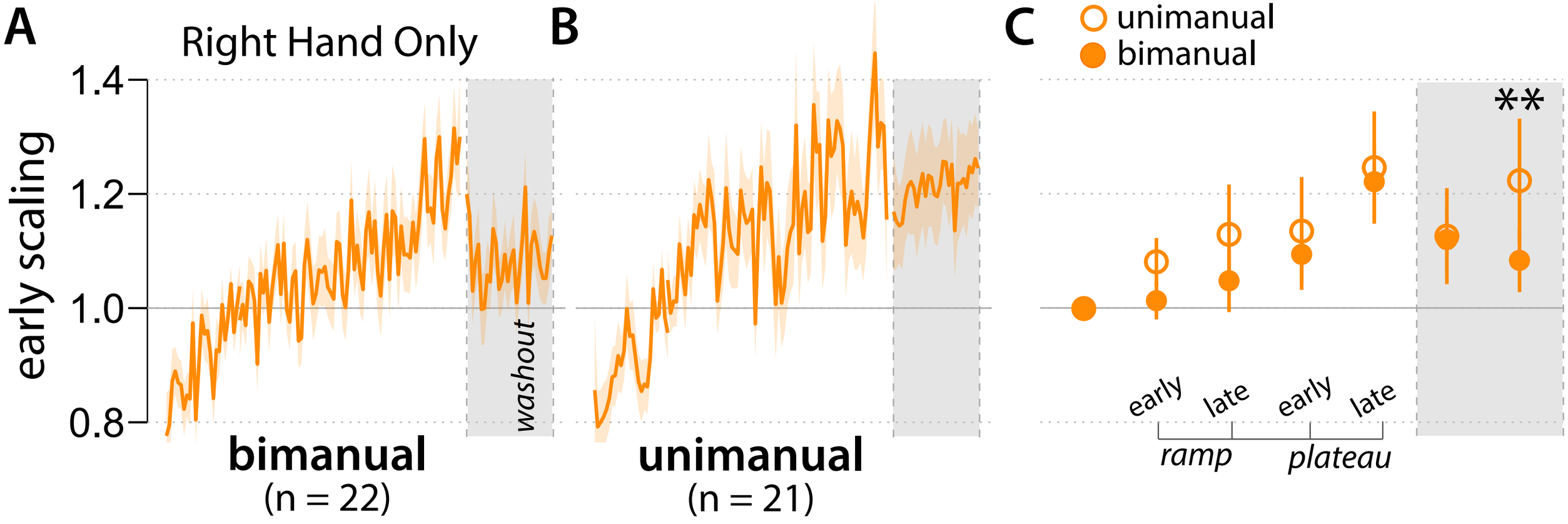

A
Meta Quest 2
LEAP motion controller
msi
+
unity
co-created with Adobe Firefly
B
Trial 2
+y
+z
+x
C
3 or 6 cm
40 cm
30 cm
26 or 13 cm
D
right hand
response
gain
trial
30 second break every 30 trials
baseline
(50 trials)
ramp down
(75 trials)
plateau
(75 trials)
washout
(60 trials)
E
right hand displacement
10 cm
500 ms
baseline
early ramp
same early speed
higher
end plateau
faster early speed
higher
early washout
faster early speed
not as high


A
Right/Left Ratio
1.4
1.2
1.0
0.8
early scaling
washout
trial
B
***
***
early
late
early
late
ramp
plateau
C
right hand
left hand
1.4
1.2
1.0
0.8
early scaling
2-trial bins
D
faster
than baseline
slower
than baseline
***
**
*
**
**
ramp
plateau


A
Right Hand Only
early scaling
1.4
1.2
1.0
0.8
washout
bimanual
(n = 22)
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unimanual
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unimanual
bimanual
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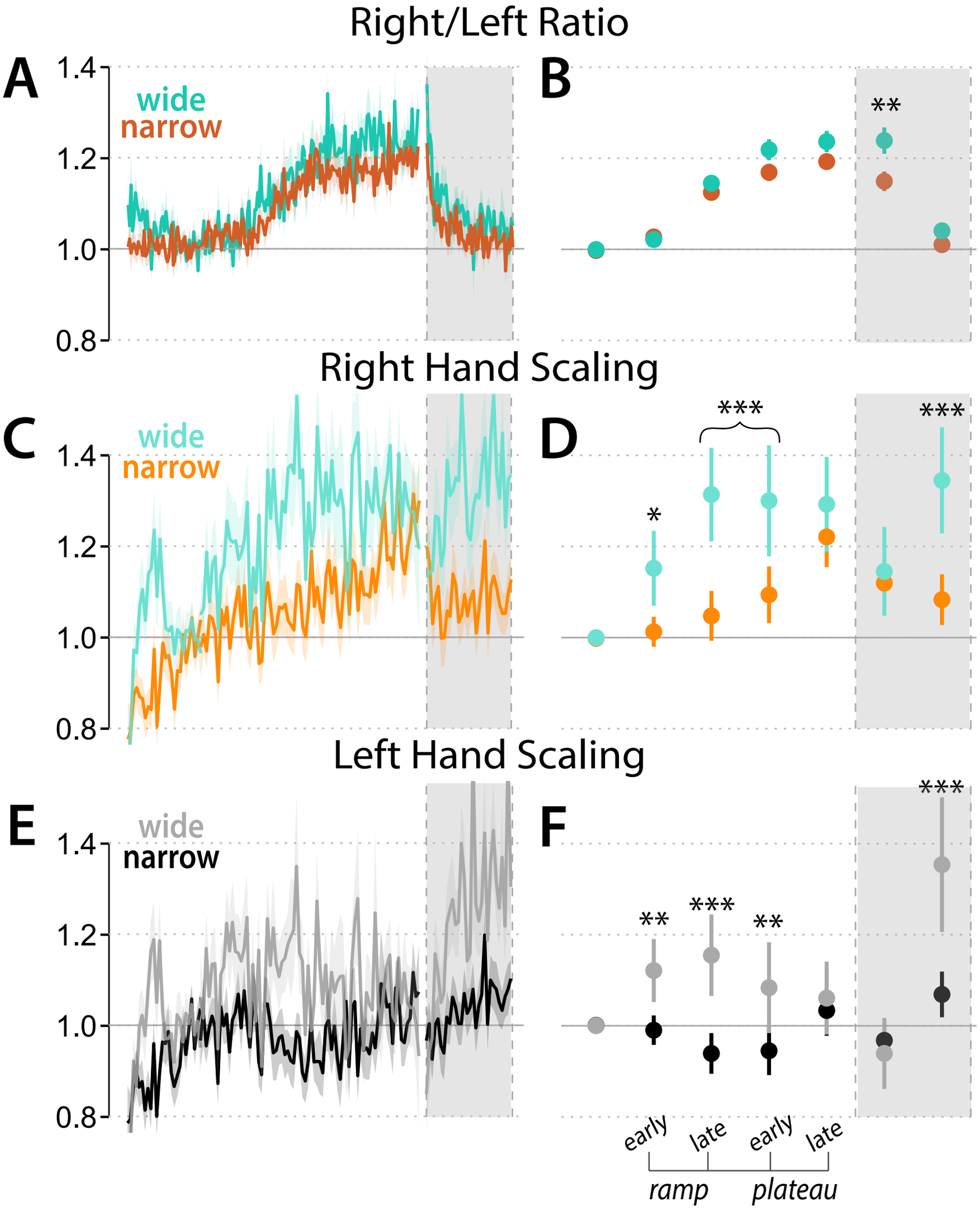
early
late
early
late
ramp
plateau


Right/Left Ratio
A
B
wide
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1.4
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Right Hand Scaling
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Left Hand Scaling
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early
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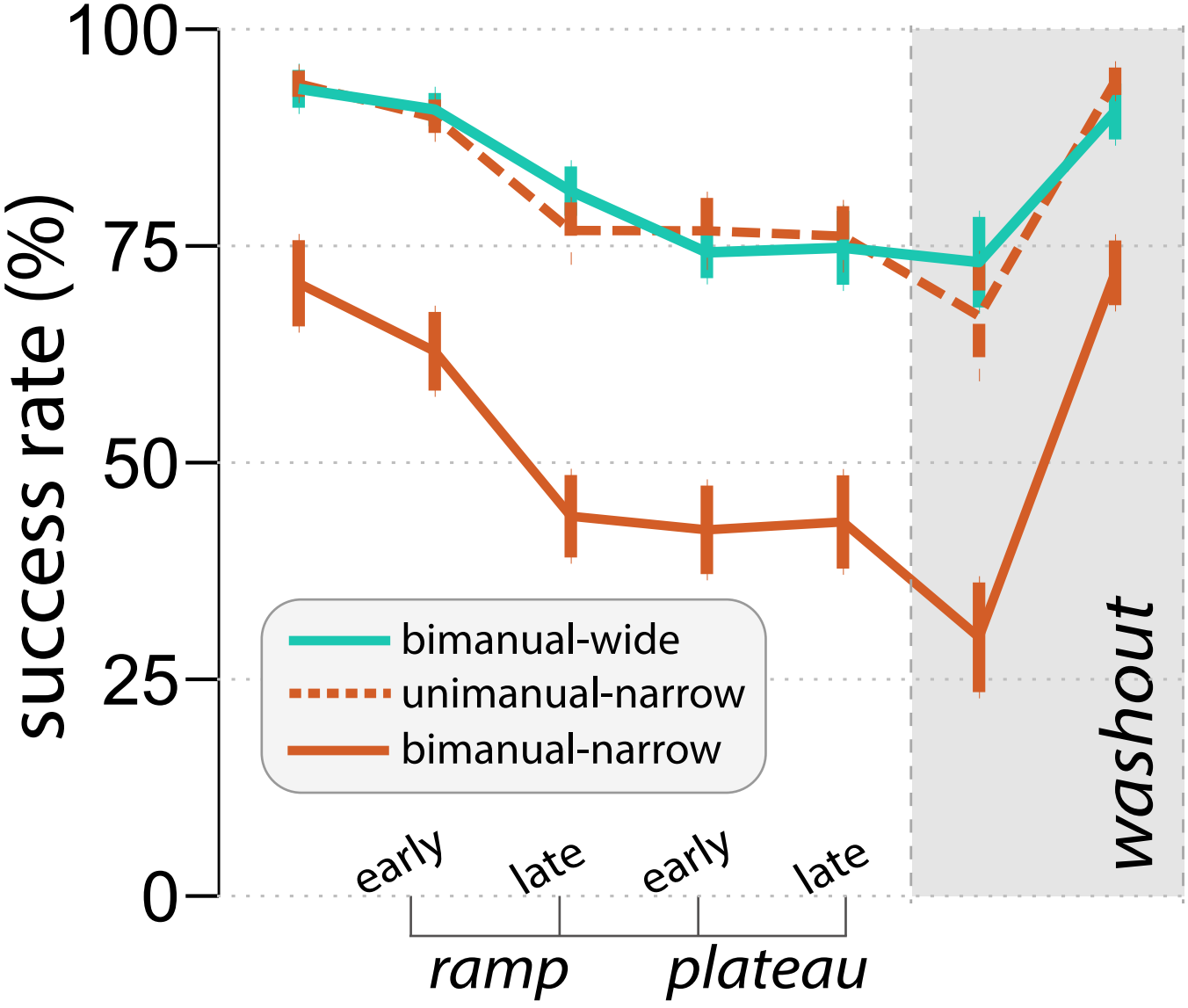
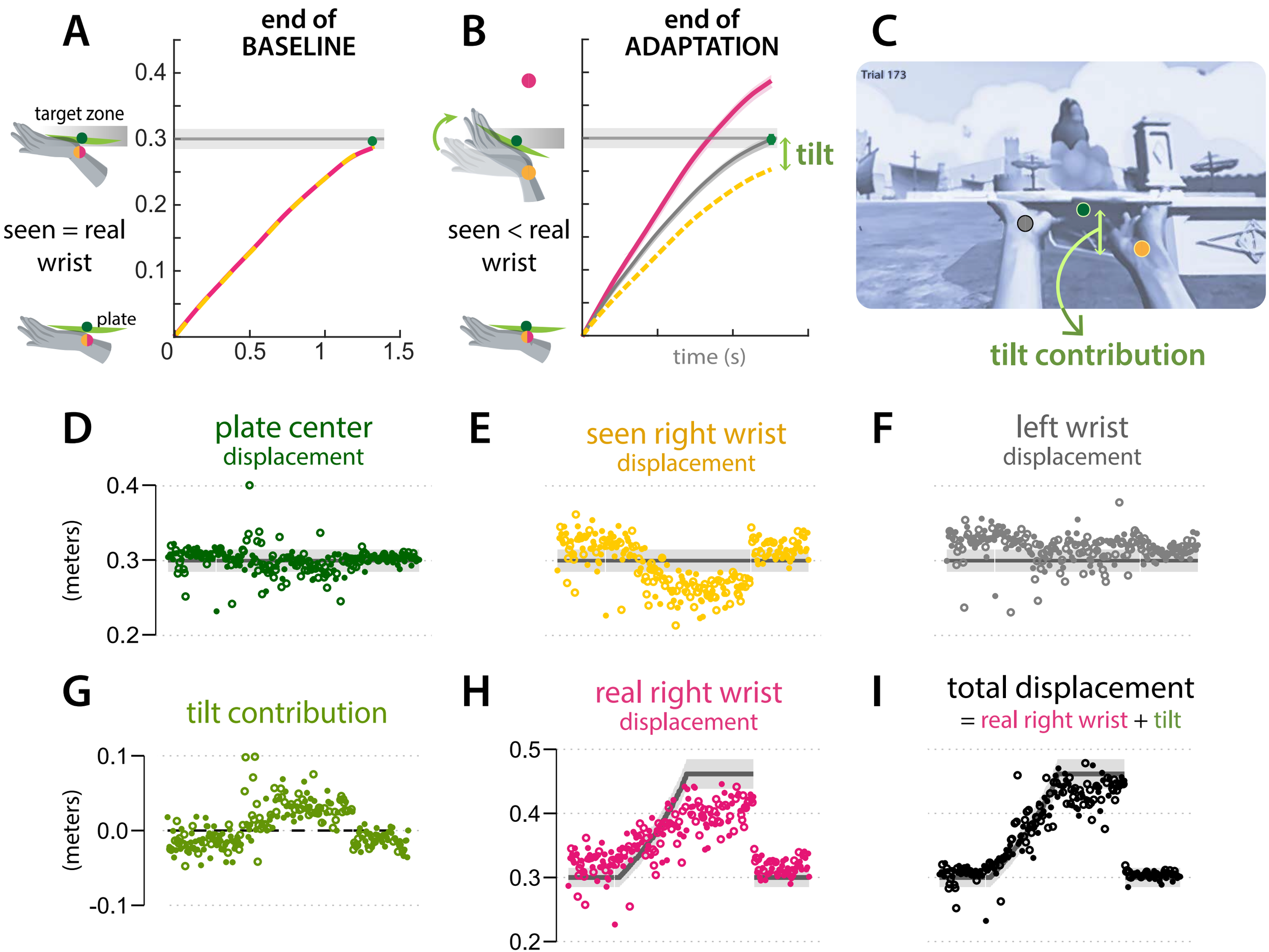
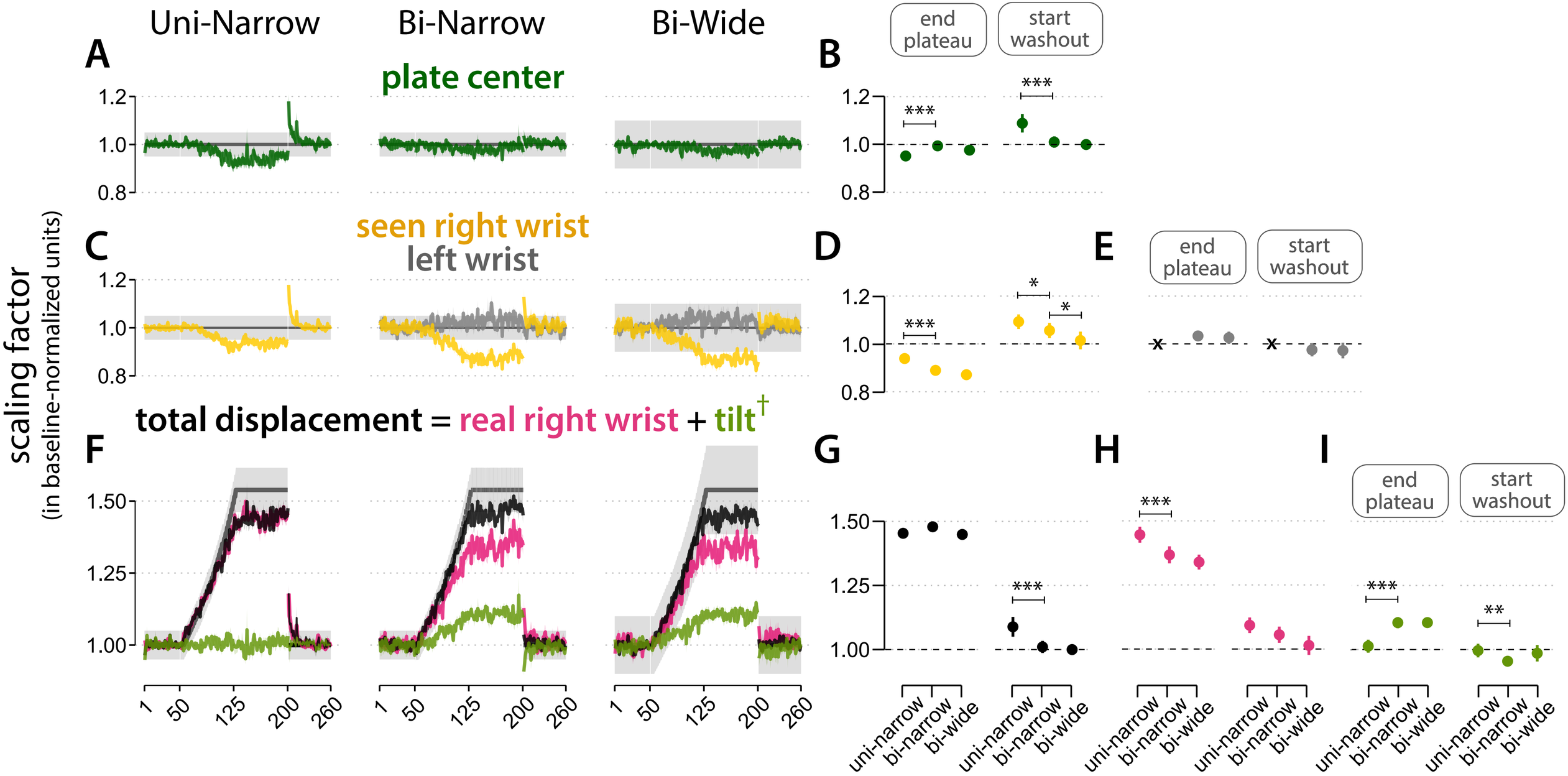

100
75
50
25
0
success rate (%)
bimanual-wide
unimanual-narrow
bimanual-narrow
early
late
early
late
ramp
plateau
washout

example from bimanual-narrow group




Uni-Narrow
Bi-Narrow
Bi-Wide
A
plate center
B
end plateau
start washout
C
seen right wrist
left wrist
D
E
total displacement = real right wrist + tilt†
F
G
H
I
scaling factor
(in baseline-normalized units)
1.2
1.0
0.8
1.50
1.25
1.00
1
50
125
200
260
***
*
**
uni-narrow
bi-narrow
bi-wide