Contrasting *de novo* learning with adaptation by the expression of aftereffects

Christopher Yang[1], Noah Cowan[1,2], Adrian Haith[3]
Departments of [1]Neuroscience, [2]Mechanical Engineering, [3]Neurology, Johns Hopkins University

New motor tasks can be learned through one of (at least) two learning mechanisms: 1) adaptation: adjustment of an existing controller, or 2) *de novo* learning: building a new controller from scratch. Classically, studies have demonstrated that adaptation to a perturbation typically leads to the expression of aftereffects when the perturbation is removed[1]. This is thought to be due to the fact that adapted controllers must be adapted back to their baseline state, which requires further experience. This framework also predicts, however, that *de novo* learning would not lead to similar aftereffects. Because *de novo* learning results in the formation of a new controller to tackle a novel motor task, existing controllers for already well-learned tasks should remain unchanged and, consequently, one should be able to quickly revert back to it when needed. Indeed, previous studies support the idea that explicit strategies can be quickly engaged and disengaged during motor learning[2]. Although aftereffects have been empirically demonstrated for adaptation, to our knowledge, the expression of aftereffects has not been tested for *de novo* learning. Here, we use the expression of aftereffects to infer whether a task is learned through adaptation or *de novo* learning.

We recruited 20 healthy, right-handed, adult human participants. Visuomotor rotation and mirror reversal have been suggested to engage adaptation and *de novo* learning, respectively[3]. Our participants therefore learned to unimanually control the movement of a cursor on a screen under one of two different visuomotor perturbations – either a 90˚ visuomotor rotation (n=10) or a mirror reversal about a 45˚ oblique axis (n=10) (Figure 1A). The 45˚ angle of the mirroring axis ensured that, under both perturbations, hand movements along the X-axis were mapped to cursor movements along the Y-axis and vice versa. Participants trained on their respective perturbations in the “point-to-point task”, in which they were required to make movements towards a series of targets appearing in random locations on the screen (Figure 1C).

We also wanted to precisely characterize improvements in participants’ control capabilities throughout training. Although we could assay learning using the point-to-point movements, the analysis of these movements can be *ad hoc* and different analytical approaches may be needed to tease visuomotor rotation and mirror reversal apart[3]. Instead, we adopted a novel method inspired by system identification, employing a “tracking task” that allowed us to measure participants’ responses to target motion at specific frequencies. The frequency-response provides a general input-output relationship for the human sensorimotor system which can (under assumptions of linearity) predict how the hand would respond to any arbitrary stimulus. In the “tracking task,” participants were required to use their cursor to track a pseudo-randomly moving, sum-of-sinusoids target (Figure 1C-D). Importantly, the frequencies of the target’s X-axis movement were different from that of the Y-axis, allowing us to isolate whether hand responses at a particular frequency were due to either X- or Y-axis target movement. This task design therefore allowed us to assess aftereffects by determining how well hand movement at a particular frequency was restricted to a single axis post-learning. We assessed learning with the tracking task at 4 timepoints: 1) Baseline, 2) Early learning 3) Late learning, and 4) Post-learning (Figure 1B).

First, to demonstrate that participants don’t simply move their hands randomly but instead genuinely attempted to track the target, we examined amplitude spectra of hand movement at baseline. Indeed, hand-movement frequencies in each axis were restricted to corresponding target-movement frequencies (Figure 2). We then assessed participants’ control capabilities at different points in learning by measuring the gain of hand movements at every target frequency (Figure 3A), where gain represents the hand-to-target amplitude ratio in the correct direction. At baseline, gain was relatively high across all frequencies for both the rotation and mirror-reversal groups. Initial exposure to the perturbation led to a significant decrease in the gain (i.e., poor tracking). However, following subsequent point-to-point training the gain returned towards baseline levels (i.e., improved tracking), though more for the rotation group. After learning, we turned off the perturbation to assess aftereffects and found the gain in the Post-learning block was slightly lower but similar to the baseline gain for both groups.

However, the gain plots in Figure 3A do not accurately reflect aftereffects; they only reflect the amplitude of hand movement in the correct direction. To better assess aftereffects, we looked at the cross-axis gain in participants’ amplitude spectra post-learning and found that the amplitude was no longer well-restricted to target frequencies (Figure 2). Spectra for only the rotation group are shown, but the mirror-reversal group exhibited significantly less cross-axis gain than the rotation group. On the basis of these cross-axis gains, we computed, at each frequency and each time point for both groups, a “compensation angle,” indicating the angle of hand movement relative to target motion (Figure 3B). An angle of 0˚ was equivalent to perfect baseline control and 90˚ was equivalent to perfect compensation under both perturbations. At baseline, the angle was close to 0˚, and training on the perturbations drove the angle towards 90˚. Following removal of the perturbation, we found that the rotation group exhibited strong aftereffects while the mirror-reversal group did not. These data substantiate our predictions, confirming that visuomotor rotations and mirror-reversals are indeed learned via distinct mechanisms[3] and supporting our conceptual framework suggesting that adaptation results in aftereffects due to a slow de-adaptation process, whereas *de novo* learning permits a quick switching process between controllers, avoiding aftereffects.

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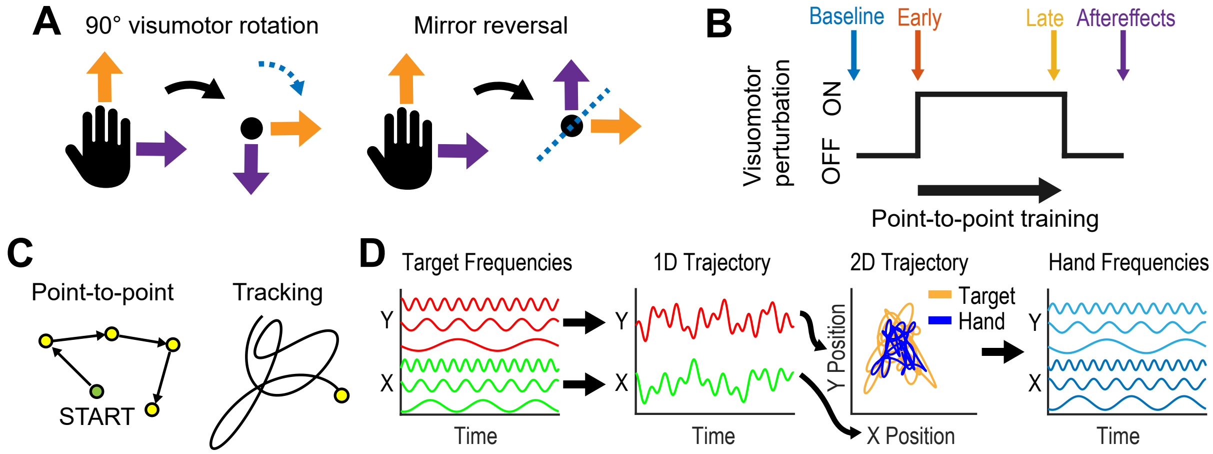
Figure 1. A) Two different visuomotor perturbations were used in this experiment, a 90° visuomotor rotation and a mirror reversal about a 45° axis. Hand movement (left) and resulting cursor movement (right) is depicted. B) We assessed participants' control capabilities at 4 stages of learning: 1) Baseline, 2) Early learning, 3) Late learning, and 4) Post-learning. C) Participants performed two different tasks while learning either of the perturbations in 1A. The majority of training was in the point-to-point task, where participants reached in discrete movements towards targets that appeared in random locations on the screen. In the tracking task, the target moved along a 2-dimensional sum-of-sinusoids trajectory, and participants tracked the target with their cursor. Participants trained on the perturbations with the point-to-point task while their learning was assessed with the tracking task. D) Simulated example of the tracking task. Participants were asked to use their right hand to track the pseudorandom (sum-of-sinusoids) motion of a target on a screen. Multiple sine waves of differing amplitudes, phases, and frequencies (far left) were summed together to create two separate 1-dimensional target trajectories (mid left). These two trajectories were summed along the X- and Y-axes to generate a 2-dimensional target trajectory (mid right), and participants' hand-tracking responses were recorded. Hand responses were decomposed into a sum-of-sinusoids by the inverse Fourier transform (far right) and compared with target sines. We focused the present analysis on the tracking task.



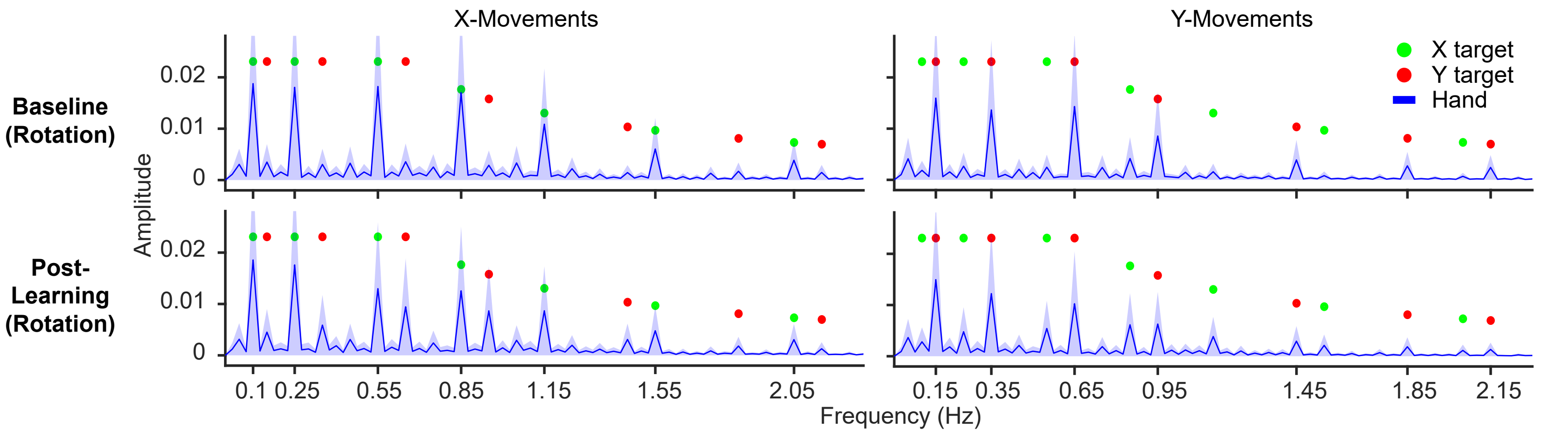


Figure 2. Amplitude spectra for the rotation group (n=10) tracking the target with veridical feedback before (Baseline: top) and after (Post: bottom) learning. Target frequencies and amplitudes are illustrated by the small circles and frequency content of the hand is plotted in blue. At baseline, the frequencies and amplitudes of hand responses were well-matched to that of the target in both the X- (left) and Y-axes (right). Importantly, the target frequencies used for the X-axis were different from that for the Y-axis, and hand movements in each axis did not reflect any frequency of movement of the other axis. Aftereffects were evident post-learning, as reflected by the cross-axis amplitude. Mirror-reversal data is not shown, but baseline behavior is similar to that of the visuomotor rotation group. Error bars are bootstrapped 95% confidence intervals.

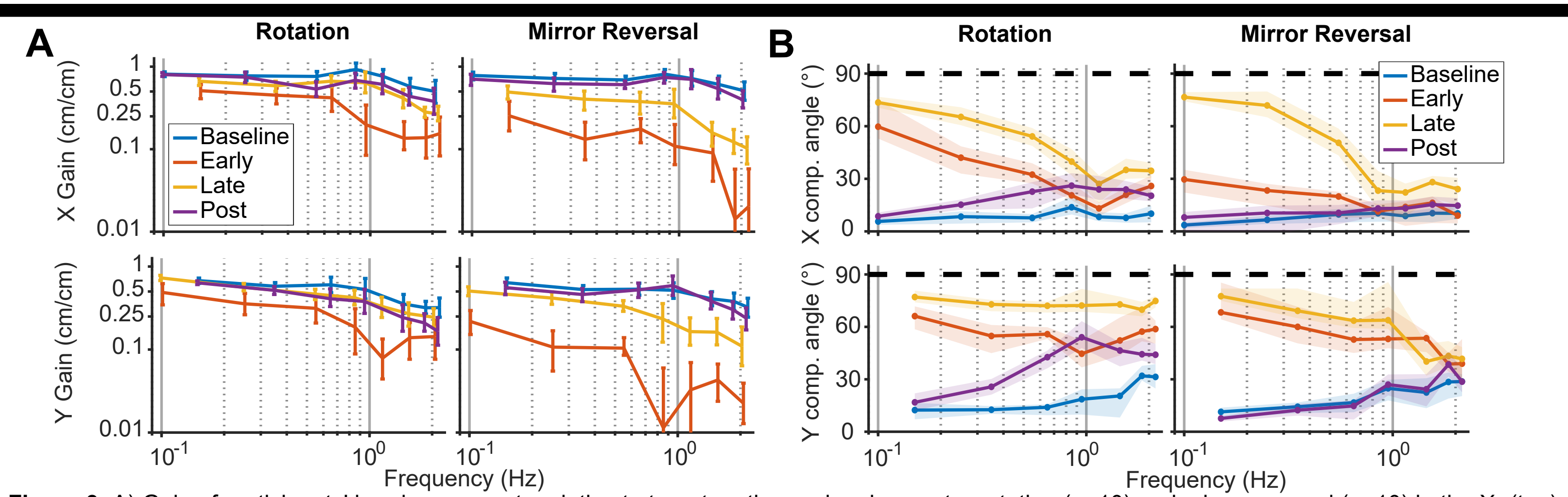


Figure 3. A) Gain of participants' hand movements relative to target motion under visuomotor rotation (n=10) and mirror reversal (n=10) in the X- (top) and Y-axes (bottom). Different frequencies are compared between blocks such that we could compare hand movements in the same axis (as opposed to cursor movements). At baseline (blue), gains were high for both groups of participants. Exposure to the perturbation reduced gain (Early: red), but training with the perturbation increased gain (Late: yellow). The mirror-reversal group exhibited a larger drop in gain during early learning. Aftereffect gain was slightly lower than baseline for both groups (Post: purple). B) We computed "compensation angle," the arctangent of the X- and Y-cursor gains at a particular frequency, to quantify cross-axis gain. With this quantification method, 0° represents perfect veridical control and 90° (dashed line) represents perfectly-compensated control for both rotation and mirror reversal. In other words, compensation angle measures the state of learning. While the compensation angle was initially close to 0° at baseline, participants were able to learn their respective perturbations (angle approached 90°). Unlike the mirror-reversal group, the rotation group exhibited strong aftereffects, as evidenced by the difference in compensation angle between the baseline and aftereffects blocks. Error bars are bootstrapped 95% confidence intervals.