

The effect of sequence learning on sensorimotor adaptation

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HIGHLIGHTS

- Sequence and sensorimotor learning are normally studied separately
- Position-dependent force field allows combined sensorimotor-sequence learning task
- Sequenced order of target positions did not reliably affect sensorimotor adaptation
- Sequenced force field directions facilitated sensorimotor adaptation and retention
- Sensorimotor and sequence learning do not monopolize each other's neural resources

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Abstract

Motor skill learning involves both sensorimotor adaptation (calibrating the response to task dynamics and kinematics), and sequence learning (executing task elements in the correct order at the necessary speed). These processes typically occur together in natural behavior and share much in common, such as working memory demands, development, and possibly neural substrates. However, sensorimotor and sequence learning are usually studied in isolation in research settings, for example as force field adaptation or serial reaction time tasks (SRTT), respectively. It is therefore unclear whether having predictive sequence information during sensorimotor adaptation would facilitate performance, perhaps by improving sensorimotor planning, or if it would impair performance, perhaps by occupying neural resources needed for sensorimotor adaptation. Here we evaluated adaptation to a position-dependent force field in two different SRTT contexts: In Experiment 1, 28 subjects reached between 4 targets in a sequenced or random order. In Experiment 2, 40 subjects reached to one target, but 3 force field directions were applied in a sequenced or random order. No consistent influence of target position sequence on force field adaptation was observed in Experiment 1. However, sequencing of force field directions facilitated sensorimotor adaptation and retention in Experiment 2. This is inconsistent with the idea that sensorimotor and sequence learning share neural resources in any mutually exclusive fashion. These findings indicate that under certain conditions, sequence learning interacts with sensorimotor adaptation in a facilitatory manner. Future research will be needed to determine what circumstances and features of sequence learning are facilitatory to sensorimotor adaptation.

Keywords: Sensorimotor adaptation; sequence learning; force field adaptation; SRTT

1 Introduction

In real-world motor skill acquisition, individuals must learn both sensorimotor and sequence aspects of the movement. Sensorimotor learning involves optimizing kinematic and dynamic parameters of a movement with sensory information. This involves learning aspects of the movement like forces and distances. For example, when a typist, fluent in typing on a modern small light-tough keyboard, is switched to an old-fashioned mechanical typewriter, typing speed and accuracy would likely drop due to sensorimotor factors such as wider spread of buttons and heavier resistances of keys. The process of compensating for such factors on a different keyboard is an example of a form of sensorimotor learning known as adaptation. In research, one of the classic sensorimotor adaptation tasks is force field adaptation (Shadmehr & Mussa-Ivaldi, 1994). The subject experiences externally-applied forces that will perturb a normal movement, such as reaching. Through trial and error practice, subjects learn to compensate for the forces, adapting to reduce reaching errors and approach their baseline level of performance. If the forces are abruptly removed, subjects who have adapted will display errors in the opposite direction, a phenomenon known as negative aftereffect. The presence of a negative aftereffect indicates that a modified relationship between motor command and expected outcome, learned during adaptation, has been stored.

In contrast with sensorimotor adaptation, sequence learning involves learning a pattern of movements that are in a repeating order and optimizing the performance. Common examples could be learning to type words or phrases that come up frequently, such as one's email address or name. This requires quickly producing the correct finger movements in the correct order. Classic laboratory sequence learning tasks such as serial reaction time task (SRTT) usually have minimal motor requirements, such as button pressing (Summers, 1975). The change in reaction

1 time is a typical measure for SRTTs, with faster reaction time indicating sequence learning.

2 Sensorimotor adaptation and sequence learning are both critical for motor skill
3 acquisition. In natural behavior, these processes most likely occur together. For example,
4 learning the sequence of footsteps and the force of each step together in a dance routine.
5 However, in the research setting, sensorimotor and sequence learning have largely been studied
6 in isolation, limiting our understanding of how these processes interact. Sensorimotor and
7 sequence learning have some properties in common, such as working memory demands and
8 implicit vs. explicit components. Anguera, Reuter-Lorenz, Willingham, and Seidler (2010) found
9 that spatial working memory is positively correlated with adaptation rate during the early stage
10 of a visuomotor rotation task, illustrating the importance of working memory in sensorimotor
11 learning. Spatial working memory has also been shown to play a role in both explicit (Bo and
12 Seidler 2009) and implicit (Bo, Jennett, and Seidler 2011) sequence learning.

13 Sensorimotor and sequence learning also rely on many of the same neural substrates. A
14 meta-analysis comparing functional magnetic resonance imaging (fMRI) studies (Hardwick,
15 Rottschy, Miall, & Eickhoff, 2013) found that both sequence and sensorimotor learning tasks
16 activated left dorsal premotor cortex, left primary motor cortex (M1), supplementary motor area
17 (SMA), and right cerebellum. In contrast, putamen was only active during sensorimotor
18 adaptation, while thalamus was active during sequence learning alone. M1 is heavily involved in
19 consolidation and retention periods of force field adaptation (Richardson et al., 2006; Hunter,
20 Sacco, Nitsche, & Turner, 2009; Galea, Vazquez, Pasricha, Orban de Xivry, & Celnik, 2011).
21 Premotor cortex is engaged in sequence learning (1998; 2000) as well as sensorimotor adaptation
22 (Kurata & Hoshi, 1999). SMA plays an important role in programming complex sequential
23 movements (Roland, Larsen, Lassen, & Skinhoj, 1980) and its activity increases throughout the

1 learning process (Grafton, Hazeltine, & Ivry, 1995; Toni et al., 1998). SMA proper is also
2 engaged in sensorimotor adaptation tasks (Gerlo & Andres, 2002; Serrien, Strens, Oliviero, &
3 Brown, 2002). Previous studies also found cerebellum involvement in both adaptation (Jayaram
4 et al., 2012; Galea et al., 2011) and sequence learning (2002) tasks.

5 While much can be deduced by comparing the results of sequence learning and
6 sensorimotor adaptation studies, many questions can only be answered by developing tasks in
7 which sensorimotor and sequence learning can be studied simultaneously, in the same
8 participants. For example, knowing that both processes depend on working memory and certain
9 brain regions does not tell us whether they interfere with or facilitate each other when occurring
10 at the same time. It is unknown whether having predictive sequence information during
11 sensorimotor adaptation facilitates performance, perhaps by improving sensorimotor planning, or
12 if it impairs performance, perhaps by occupying neural resources needed for sensorimotor
13 adaptation.

14 Here we asked whether the addition of a sequence component facilitates sensorimotor
15 adaptation in healthy adults. If sensorimotor adaptation improves when there is an embedded
16 sequence component, it would suggest a beneficial interaction that could one day be taken
17 advantage of in motor rehabilitation for clinical populations with impaired movement, such as
18 stroke. If sensorimotor adaptation worsens when there is a sequence component, it would suggest
19 a detrimental interaction, perhaps due to the monopolizing of shared resources, that requires
20 further study. Should sequence learning have no effect on sensorimotor adaptation, it would
21 suggest these two motor skill systems operate independently in behavior. Because it is unknown
22 what type of sequence component might affect sensorimotor adaptation, we tested two.
23 Experiment 1 tested the effect of sequenced target positions in force field adaptation, while

Experiment 2 tested the effect of sequenced force field directions on force field adaptation.

2 Materials and Methods

2.1 Participants

Typically developing adults participated in both experiments. Twenty-eight individuals aged 24.11 ± 6.22 years old participated in Experiment 1, and 40 adults aged 22.50 ± 4.72 years old participated in Experiment 2 (mean $\pm$ SD). In Experiment 1, 25 subjects were classified as right-handed and 3 left handed according to the Edinburgh handedness inventory (Oldfield 1971). All 40 participants in Experiment 2 were classified as right-handed. All participants reported no history of neurological disorders or upper limb muscular injuries. All participants gave written informed consent. The study was approved by the institutional review board of Indiana University Bloomington.

2.2 Apparatus

Participants performed reaching movements on a robotic apparatus (KINARM End-Point Lab, BKIN Technologies, Kingston, Canada). The KINARM system uses a 2D virtual reality display to present visual stimuli (Fig. 1Ai). A downward facing TV on top projected tasks onto the mirror. Participants were seated in front of the apparatus and grasped the robotic manipulandum. Participants viewed the task display in the mirror, which prevented vision of the hand and manipulandum. The task display appeared to be in the same horizontal plane as the robotic manipulandum. A drape over the shoulders prevented participants from seeing their upper arm and shoulder. Veridical visual feedback of the hand's position was provided as a white dot in the task display. The reaching tasks were programmed using Simulink toolbox from MATLAB 2017b (MathWorks Inc., Natick, MA, United States). Tasks were operated, and data

was stored through the operation and acquisition software Dexterit-E by BKIN Technologies.
The sampling rate for hand position and force was 2,000HZ.

2.3 Force field design

Force field adaptation in reaching is commonly studied with a velocity dependent force field perturbation, where the amount of force is directly related to the subject's movement velocity (Shadmehr & Mussa-Ivaldi, 1994). However, this type of force field could create a confound in a sequence-learning study: Subjects might move faster as they learn the sequence, which would result in stronger force perturbations, interfering with sensorimotor adaptation. We therefore developed a novel position-dependent force field, designed to apply the same pattern of forces regardless of subjects' movement velocity.

First we computed the vector from the end target to start target (SE):

$$\vec{SE} = e - s$$

where e and s were the vectors for start and end targets; we computed γ , which was the force angle perpendicular to the SE vector:

$$\gamma = \arctanh(\vec{SE}) + \frac{\pi}{2}$$

f_x and f_y were the lateral (x) and sagittal (y) directions of the maximum manipulandum force magnitudes:

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = K \begin{bmatrix} \cos \gamma \\ \sin \gamma \end{bmatrix}$$

where K is 18 N. $\cos \theta$ was the angle between the reaching hand and the start target and the start and end targets.

$$\cos \theta = \frac{\vec{SH} \cdot \vec{SE}}{\|\vec{SH}\| \|\vec{SE}\|}$$

where $\vec{SH}$ was the vector for start target and reaching hand positions. The ratio of the projection of the reaching hand onto the line defined by the start and end targets was then determined. f'_x and f'_y were the manipulandum forces at hand position:

$$\begin{bmatrix} f'_x \\ f'_y \end{bmatrix} = \frac{\sin\left(\frac{\|\vec{SH}\| - \cos\theta}{\|\vec{SE}\|} \cdot \pi\right)}{\sqrt{2}} \begin{bmatrix} f_x \\ f_y \end{bmatrix}$$

To mimic the reaching pattern of a velocity-dependent force field, we scaled the force field into a bell shape. The force field was gradually introduced as the reaching hand left the start target, maximized half-way through the reach, and gradually dialed down as the hand got closer to the end target (Fig. 1Aii). The maximum applied force was 12.7 N. In other words, participants experienced the same scale of external force during reaching regardless of hand movement velocity or target direction. However, subjects could experience different amounts of impulse (integral of force over time), as this parameter would be affected by movement time (Cashaback et al., 2015). Participants did not experience any force or resistance while their hand was in a target.

2.4 Experimental Procedure

After signing the informed consent form, participants completed the Edinburgh Handedness Inventory (Oldfield, 1971) to determine which hand would be the dominant hand in performing the reaching task. Participants were randomly assigned to one of the groups in the experiment.

Participants were seated in front of the robotic apparatus (Fig. 1Ai). They were instructed to move the robotic manipulandum briskly to a target in a straight line, using their dominant hand. When a target turned green, it signaled the participant to start reaching towards it. Once the

hand arrived at the target, the color turned red and participants were asked to hold the manipulandum within the target until the next target turned green. The wait time for the next target to appear was randomly chosen from the range 500 to 1500 ms. A real-time white dot representing the participant's hand was visible during both experiments. Participants were familiarized with the task by a practice block with no force or sequence.

Participants were not informed of when and where the force field would be onset and participants were also not given any hint regarding the possible existence of a sequence. The experimenter asked participants whether they noticed any pattern or sequence upon experiment completion. If answered yes, the experimenter would ask the participants to describe what they noticed. For experiment 1, if the participant noticed sequence of reach directions or target appearances, the experimenter would provide an image of the task layout (Fig. 1Bi) and ask the participant to draw the remembered sequence. For experiment 2, if participants noticed the different force directions or sequence of the force directions, the experimenter recorded the order they recalled.

2.4.1 Experiment 1

The task displayed four 1cm-diameter hollow circles as the targets on the screen, located at the four corners of a 20cm square (Fig. 1Bi). Two targets were displayed on the participant's midline. The other two targets were on the right side of the display for right-handed subjects, or the left side of the display for left-handed subjects. In total, the reaching task had 40 epochs. Each epoch consisted of 12 reaching movements, covering the 12 different possible reach directions between the 4 targets (Figure 1.B.i). Thus, the entire task contained 480 reaching movements. After each epoch, the total movement time across all 12 reaches was displayed on the screen to give participants a general idea about their speed. This served as a reminder to

avoid significant slowing down later in the experiment due to fatigue or boredom.

Participants were randomly assigned to a sequence group ($n = 16$), where the epoch of 12 targets appeared in a particular order and participants experienced a force field, or a random group ($n = 12$), where targets appeared in a random order, but participants still experienced a force field. For both groups, each epoch of 12 reaches started and ended at the same target (T1, top mid-line target). The first block was a baseline consisting of five epochs in a null field, with the targets presented in random order (Fig. 1Bii). The second block was an adaptation block (25 epochs) with the force field on. Target order either continued in random order (random group) or began following a repeating sequence. In the 13th of 25 adaptation epochs, the force field was turned off unexpectedly for the 5th reach. This catch reach was implemented to confirm subjects were attending (Shadmehr & Brasher-Krug, 1997). Finally, the washout block contained 10 epochs with no force perturbation; the sequence group continued to experience the same sequence. For the sequence group, beginning in the adaptation block, the targets in each epoch appeared in a fixed order: T1-T4 (Reach 1), T4-T2 (Reach 2), T2-T3 (Reach 3), T3-T4 (Reach 4), T4-T1 (Reach 5), T1-T3 (Reach 6), T3-T1 (Reach 7), T1-T2 (Reach 8), T2-T4 (Reach 9), T4-T3 (Reach 10), T3-T2 (Reach 11), T2-T1 (Reach 12).

2.4.2 Experiment 2

All reaches were straight-ahead, with two targets aligned on the participant's midline. The start target was closer to the participant and the end target was 20 cm forward of the start target. Participants were instructed to make straight and brisk movements from start to end target. After reaching the end target, the robot automatically brought the testing arm back to the start target for the next epoch. There were three force directions pushing to the dominant hand side of the participant: a horizontal direction (0° perpendicular to the straight line between start and end

targets), a 45° upward direction, and a 315° downward direction (Fig. 1Ci). During the adaptation blocks, every epoch of 6 reaches included two of each force direction. For analysis purposes, reaches in baseline and washout blocks were also grouped into epochs of 6 reaches.

Participants were randomly assigned to one of two groups: a sequenced force directions group and a random force directions group. The task was divided into five blocks. The first was a baseline block where no force was applied (4 epochs of 6 reaches). The baseline was followed by an adaptation block (30 epochs of 6 reaches), in which both groups experienced a position-dependent force field. For the sequence group, each epoch included the three directions of force in the order: 0° , 45° , 315° , 0° , 315° , 45° . Adaptation was followed by the first washout block (7 epochs of 6 reaches), in which no forces were applied (null force). In the second adaptation block (15 epochs of 6 reaches), the settings of force field and directions were the same as the first adaptation block. The second washout block (4 epochs of 6 reaches) was performed in the null field (Fig. 1Cii). 17 participants performed an earlier version of the task, in which the baseline block was 20 reaches, washout 1 was 40 reaches, and washout 2 was 20 reaches.

2.5 Outcome variables and analysis

All data were preprocessed and analyzed using MATLAB. Outcome measures from the manipulandum data were maximum perpendicular deviation, movement time, and reaction time. We also computed force impulse for adaptation trials. Perpendicular deviation is the distance between the hand reaching trajectory to the straight line between the two targets. The maximum perpendicular deviation can thus be used as a measure of sensorimotor error (Darainy & Ostry, 2008). Max perpendicular deviation for each epoch was determined by averaging max perpendicular deviation across reaches within that epoch (12 reaches in Experiment 1 and 6

reaches in Experiment 2). Max perpendicular deviations in adaptation and washout blocks were normalized by subtracting the last epoch in the baseline block. Movement time was the time between leaving the start target and entering the end target. Movement time for each epoch was determined by averaging movement time across reaches within that epoch. Reaction time was measured as the time from target onset to movement being detected (the moment the hand left the start target). We computed force impulse for adaptation block reaches as the integral of applied force over time (Cashaback et al., 2015) . To compare the rate of adaptation during force field blocks, we defined early adaptation to be reaches 2 - 11 in the adaptation blocks in both experiments (Lamothe et al., 2014). These reaches occurred in epoch 1 for Experiment 1, and epochs 1 and 2 for Experiment 2. We did not include the first reach because the unexpected onset of the force field could surprise subjects. We calculated the linear slope of reaches 2-11 as the early adaptation rate (Diedrichsen, 2007) and compared across groups with an independent-sample t-test.

To compare max perpendicular deviation, two-way mixed model ANOVAs were performed on each adaptation and washout block, with within-subjects factor “time” (epochs or reaches in block) and between-subjects factor “group” (sequence vs. random group). Movement time and impulse were analyzed the same way for each adaptation block, to determine whether individual differences in movement time or impulse could have resulted in different force impulses during adaptation. Two-way mixed model ANOVA was used to analyze change of reaction time from pre to post sequence learning. The between-subjects factor “group” was the sequence vs. random group. The within-subjects factor “time” was the first and last epochs in the adaptation blocks. We performed post-hoc Tukey t-tests comparing reaction time within groups upon finding a significant interaction. We computed generalized eta squared (η_G^2) as an effect

size for all ANOVA effects, as this parameter is recommended for ANOVA designs that include repeated measures (Bakeman, 2005). We computed Cohen's d as an effect size for t-tests. Hypothesis tests were performed two-sided with α of 0.05.

3 Results

3.1 Experiment 1

3.1.1 Sensorimotor learning

Figure 1.B.ii shows movement paths of an example participant. During the baseline block, the movement paths showed very few errors. When the force field was first onset in the adaptation block, the movement paths deviated from the straight line between targets. After trial-and-error practice, movement paths in the last epoch of the adaptation block showed fewer errors, similar to the path pattern in the baseline epoch, which indicates adaptation occurred. When the external force was just turned off at the beginning of the washout block, we observed large deviations to the opposite side of the first adaptation epoch, reflecting a negative aftereffect.

Comparing normalized perpendicular deviation per epoch (error averaged across reach direction) between the sequence and random groups revealed no differences in sensorimotor adaptation (Fig. 2A). In the adaptation block there was a significant main effect of time ($F_{24, 624} = 63.51, p < 0.0001, \eta_G^2 = 0.45$), consistent with trial-by-trial error reduction. However, there was no effect of group ($F_{1, 624} = 0.41, p = 0.53, \eta_G^2 = 0.010$) or group by time interaction ($F_{24, 624} = 0.85, p = 0.68, \eta_G^2 = 0.011$). The washout block also had a main effect of time ($F_{9, 234} = 180.05, p < 0.0001, \eta_G^2 = 0.77$), consistent with a negative aftereffect. There was no group ($F_{1, 234} = 0.37, p = 0.55, \eta_G^2 = 0.007$) or group by time interaction ($F_{9, 234} = 0.34, p = 0.96, \eta_G^2 = 0.006$) for the

washout block. Comparing the catch reach between the two groups found no significant difference ($t_{26} = -1.51, p = 0.14, d = 0.58$). Early adaptation rate was not significantly different between the two groups either ($t_{26} = -0.45, p = 0.66, d = 0.17$) (Fig. 2A inset and Fig. 2D). Movement time during the adaptation block (Fig. 2B) had a main effect of epoch ($F_{24,624} = 13.32, p < 0.0001, \eta_G^2 = 0.15$), but no effect of group ($F_{1,624} = 2.29, p = 0.14, \eta_G^2 = 0.054$) or group by epoch interaction ($F_{24,624} = 0.83, p = 0.71, \eta_G^2 = 0.011$). Force impulse during the adaptation block (Fig. 2C) also had a main effect of epoch ($F_{24,624} = 6.90, p < 0.0001, \eta_G^2 = 0.090$), but no effect of group ($F_{1,624} = 0.81, p = 0.38, \eta_G^2 = 0.019$) or group by epoch interaction ($F_{24,624} = 1.32, p = 0.14, \eta_G^2 = 0.018$).

Examining individual reach directions, rather than averaging perpendicular error across the 12 directions in each epoch, revealed some group differences (Fig. 3). Among the four vertical reach directions (Fig. 3A), there was a significant interaction of group and time for reach direction 5 in washout ($F_{9,234} = 2.05, p = 0.035, \eta_G^2 = 0.024$). There was also a significant main effect of group for reach direction 1 in washout ($F_{1,234} = 8.22, p = 0.0081, \eta_G^2 = 0.17$). Significant main effects of time were observed in adaptation ($p < 0.0001$) as well as washout ($p < 0.0001$). Among the four diagonal reach directions (Fig. 3B), a significant group and time interaction was found for reach direction 9 in adaptation ($F_{24,624} = 1.83, p = 0.0094, \eta_G^2 = 0.025$). For reach directions 2, 7, and 9, the main effects of group were significant in adaptation ($F_{1,624} = 4.59, p = 0.042, \eta_G^2 = 0.091$; $F_{1,624} = 8.98, p = 0.0059, \eta_G^2 = 0.078$; $F_{1,624} = 4.27, p = 0.049, \eta_G^2 = 0.095$). The main effects of group for reach directions 2 and 7 were also significant in washout ($F_{1,234} = 4.20, p = 0.050, \eta_G^2 = 0.088$; $F_{1,234} = 4.53, p = 0.043, \eta_G^2 = 0.12$). All four diagonal reach directions had significant main effects of time in both adaptation ($p < 0.0001$) and washout ($p < 0.0001$). Among the four horizontal reach directions (Fig. 3C), a significant

interaction of group and time was found for reach direction 8 in adaptation ($F_{24, 624} = 1.65, p = 0.027, \eta_G^2 = 0.025$). For reach directions 4, 8, and 10 in adaptation, there were significant main effects of time ($F_{24, 624} = 1.77, p = 0.014, \eta_G^2 = 0.024$; $F_{24, 624} = 1.88, p = 0.0071, \eta_G^2 = 0.028$; $F_{24, 624} = 8.03, p < 0.0001, \eta_G^2 = 0.14$). All four horizontal reach directions had significant main effects of time in washout ($p < 0.0001$). Reaches were grouped according to the reaching order in the sequence group (Fig. 1Bi).

3.1.2 Sequence learning

13 out of 16 participants in the sequence group were able to recognize at least part of the sequence. The average number of sequence elements recognized was 5.3 ± 2.5 (mean $\pm$ 95% CI) in the sequence group. Reaction time of first (onset of sequence exposure) and last (final repetition of sequence) epoch in sequence learning were compared between the sequence and random groups. There was a significant interaction of time and group ($F_{1, 26} = 8.29, p = 0.0079, \eta_G^2 = 0.058$), suggesting the sequence group's reaction time decreased due to sequence learning relative to the random group (Fig. 2E). We confirmed that the sequence group's reaction time decreased significantly ($t_{15} = 4.81, p = 0.0002$). There was a main effect of time ($F_{1, 26} = 13.98, p = 0.00092, \eta_G^2 = 0.095$), but no effect of group ($F_{1, 26} = 1.38, p = 0.25, \eta_G^2 = 0.041$).

3.2 Experiment 2

3.2.1 Sensorimotor adaptation

Figure 1.C.ii shows example movement paths of a participant in each block of Experiment 2. Little movement error was observed during the baseline block. When the force field was first onset in the two adaptation blocks, hand trajectories were substantially deviated from the straight line. Through trial-and-error practice, the last few epochs in the adaptation block showed smaller deviation from the straight line. When the external force was just removed in the two washout

1 blocks, large deviations were observed to the opposite side of the adaptation reaches, indicating a
2 negative aftereffect.

3 We compared perpendicular deviation between the two groups in the baseline block and
4 found no effect of time ($F_{3,114} = 2.22, p = 0.089, \eta^2 = 0.024$), group ($F_{1,114} = 0.06, p = 0.81, \eta^2 =$
5 0.001) or group and time interaction ($F_{3,114} = 0.98, p = 0.40, \eta^2 = 0.006$). We then normalized
6 each epoch in the remaining four blocks by subtracting individuals' mean baseline perpendicular
7 deviation (Fig. 4A). There was a main effect of time in the first adaptation block ($F_{29,1102} = 65.39,$
8 $p < 0.0001, \eta^2 = 0.52$), reflecting that both groups reduced perpendicular error across epochs as
9 expected. A significant interaction between group and time in the first adaptation block ($F_{29,1102} =$
10 $1.64, p = 0.018, \eta^2 = 0.027$) suggests that the two groups reduced error at different rates, with a
11 small effect size (Bakeman, 2005). There was no main effect of group ($F_{1,1102} = 0.38, p = 0.54, \eta^2$
12 $= 0.004$). In the second adaptation block, there was a significant main effect of time ($F_{14,532} = 57.29,$
13 $p < 0.0001, \eta^2 = 0.40$), indicating further adaptation took place, but no group effect ($F_{1,532} = 0.32,$
14 $p = 0.57, \eta^2 = 0.005$) or interaction ($F_{14,532} = 1.00, p = 0.45, \eta^2 = 0.012$). Early adaptation rate
15 was not significantly different between sequence and random groups in the first adaptation block
16 ($t_{38} = 1.69, p = 0.10, d = 0.53$), but did differ between groups in the second adaptation block ($t_{38} =$
17 $3.13, p = 0.0034, d = 0.99$) (Fig. 4A inset and Fig. 4D).

18 In the first washout block, there were main effects of time ($F_{6,228} = 147.58, p < 0.0001, \eta^2$
19 $= 0.61$), consistent with a negative aftereffect, and group ($F_{1,228} = 8.76, p = 0.0053, \eta^2 = 0.12$),
20 with the sequence group appearing to have a more enduring negative aftereffect. There was no
21 interaction ($F_{6,228} = 0.58, p = 0.75, \eta^2 = 0.006$). In the second washout block, there was again a
22 main effect of time ($F_{3,114} = 132.69, p < 0.0001, \eta^2 = 0.57$) and group ($F_{1,114} = 13.23, p = 0.00081,$
23 $\eta^2 = 0.18$), but no interaction ($F_{3,114} = 1.99, p = 0.12, \eta^2 = 0.019$). The effect size of the group

1 difference is considered medium for both washout blocks (Bakeman, 2005). We calculated that
2 across the epochs of the first washout block, the sequence group retained 3.6 mm more of the
3 negative aftereffect than the random group did. For the second washout block, this value was 4.8
4 mm. For comparison, the magnitude of negative aftereffect in the first epoch of both washout
5 blocks was about 20 mm.

6 Movement time during the adaptation blocks (Fig. 4B) was not associated with group. In
7 the first adaptation block, there was a significant main effect of epoch ($F_{29,1102} = 4.92$, $p < 0.0001$,
8 $\eta_G^2 = 0.029$). However, there was no effect of group ($F_{1,1102} = 0.21$, $p = 0.65$, $\eta_G^2 = 0.0043$) and no
9 group by epoch interaction ($F_{29,1102} = 0.76$, $p = 0.82$, $\eta_G^2 = 0.0045$). Similarly, in the second
10 adaptation block, there was a significant main effect of epoch ($F_{14,532} = 5.19$, $p < 0.0001$, $\eta_G^2 =$
11 0.021), but no effect of group ($F_{1,532} = 0.81$, $p = 0.37$, $\eta_G^2 = 0.018$) and no group by epoch
12 interaction ($F_{14,532} = 1.15$, $p = 0.31$, $\eta_G^2 = 0.0047$). Similarly, impulse during the adaptation blocks
13 (Fig. 4C) was not associated with group. There was a significant main effect of epoch in both
14 adaptation blocks ($F_{29,1102} = 1.54$, $p = 0.034$, $\eta_G^2 = 0.009$; $F_{14,532} = 4.88$, $p < 0.0001$, $\eta_G^2 = 0.016$).

15 We also separately examined the perpendicular deviation from each of the three force
16 directions in the two adaptation blocks (Fig. 5). In the 0° horizontal force direction reaches (F1,
17 Fig. 1Ci), we found significant main effect of time for both adaptation blocks ($F_{29,1102} = 92.93$, p
18 < 0.0001 , $\eta_G^2 = 0.62$; $F_{14,532} = 75.62$, $p < 0.0001$, $\eta_G^2 = 0.57$), suggesting subjects in both groups
19 adapted to this force field direction (Fig. 5A). We also found main effects of group ($F_{1,1102} = 32.97$,
20 $p < 0.0001$, $\eta_G^2 = 0.22$; $F_{1,532} = 44.19$, $p < 0.0001$, $\eta_G^2 = 0.29$), and group by time interactions
21 ($F_{29,1102} = 8.79$, $p < 0.0001$, $\eta_G^2 = 0.14$; $F_{14,532} = 13.70$, $p < 0.0001$, $\eta_G^2 = 0.19$), suggesting
22 differences between the sequence and random groups.

23 In the 45° up-right force direction reaches (F2, Fig. 1Ci), both adaptation blocks had a main

effect of time ($F_{29,1102} = 31.40$, $p < 0.0001$, $\eta_G^2 = 0.37$; $F_{14,532} = 21.18$, $p < 0.0001$, $\eta_G^2 = 0.25$) and a group by time interaction ($F_{29,1102} = 11.31$, $p < 0.0001$, $\eta_G^2 = 0.17$; $F_{14,532} = 12.93$, $p < 0.0001$, $\eta_G^2 = 0.17$), suggesting the groups changed differently over time in both adaptation blocks (Fig. 5B). However, there was no main effect of group in either adaptation block ($F_{1,1102} = 2.66$, $p = 0.11$, $\eta_G^2 = 0.020$; $F_{1,532} = 1.13$, $p = 0.29$, $\eta_G^2 = 0.011$).

In the 335° down-right force direction reaches (F3, Fig. 1Ci), we found a significant main effect of time in both adaptation blocks ($F_{29,1102} = 17.54$, $p < 0.0001$, $\eta_G^2 = 0.27$; $F_{14,532} = 18.02$, $p < 0.0001$, $\eta_G^2 = 0.24$). There was also a main effect of group ($F_{1,1102} = 162.80$, $p < 0.0001$, $\eta_G^2 = 0.45$; $F_{1,532} = 120.12$, $p < 0.0001$, $\eta_G^2 = 0.50$), and a significant group by time interaction ($F_{29,1102} = 14.15$, $p < 0.0001$, $\eta_G^2 = 0.23$; $F_{14,532} = 17.56$, $p < 0.0001$, $\eta_G^2 = 0.24$) in each adaptation block (Fig. 5C).

3.2.2 Sequence learning

In both groups, many participants noticed the forces were different, but only a few perceived that there were three force directions. 17 out of 20 participants in the sequence group noticed different force directions, and the average number of directions reported was 1.90 ± 0.48 (mean $\pm$ 95% CI). 7 sequence participants were also able to recall at least half of the sequence. In the random group, 18 out of 20 participants noticed the different force directions. On average, participants in the random group reported 1.55 ± 0.39 different force directions. We compared reaction time across sequence and random groups between the first epoch (6-element sequence onset) in adaptation 1 and the last epoch in adaptation 2 (sequence ended). A significant interaction of time and group was found ($F_{1,38} = 4.88$, $p = 0.033$, $\eta_G^2 = 0.032$), suggesting reduced reaction time (sequence learning) in the sequence group relative to the random group ($t_{19} = 2.33$, $p = 0.031$) (Fig. 4E). There was no main effect of time ($F_{1,38} = 1.63$, $p = 0.21$, $\eta_G^2 = 0.012$) or group ($F_{1,38} =$

1 0.16, $p = 0.69$, $\eta_G^2 = 0.0032$).

2 **4 Discussion**

3 Here we asked whether adding a sequence component would facilitate sensorimotor
4 adaptation. We tested this idea in two ways: Sequencing of target positions in space (experiment
5 1) and sequencing of force field directions (experiment 2). We did not observe any consistent
6 influence of target position sequence on force field adaptation in experiment 1. However,
7 sequencing of force field directions facilitated the adaptation speed and increased retention in
8 experiment 2. These findings indicate that under certain conditions, sequence learning may interact
9 with sensorimotor adaptation in a facilitatory manner.

10 **4.1 Reaction time decreased among sequence groups during reaching**

11 We observed a decrease in reaction time for the sequence, but not random, group in both
12 experiments. This suggests that subjects were able to learn the sequence, whether it was a sequence
13 of target positions in experiment 1 or of force field directions in experiment 2. Classic button-press
14 serial reaction time tasks (Nissen & Bullemer, 1987; Willingham, Nissen, & Bullemer, 1989)
15 evaluate sequence learning as the change in response time, which is movement onset time (OT)
16 plus movement time (MT). However, sequence learning is difficult to distinguish from skill
17 improvement in such a paradigm, as the change in response time is the result of both OT and MT.
18 More recent approaches are able to distinguish sequence learning from sensorimotor skill learning
19 by making the time of movement onset and the end of the movement into two recordable events.
20 This allows examination of OT for sequence learning and MT for sensorimotor adaptation. For
21 example, Moisello et al. (2009) conducted a sequence learning study using visuomotor reaching.
22 They successfully tracked both OT and MT by having subjects move their finger from one target
23 to another on a tablet, with the targets appearing either sequentially or randomly. Though they

1 found a similar pattern of changes in response time to classic button-press SRTTs, the decrease in
2 response time was largely due to skill improvement, as the MT reduced during sequence learning.
3 Meanwhile, the increase of response time in a random trial during sequence learning was due to
4 the increase of OT. This means response time might not be a good measure of sequence learning
5 in reaching tasks.

6 In the current study, we used a robotic reaching tasks to extract OT (reaction time) out of
7 response time, so we were able to investigate the sequence learning component in the force field
8 adaptation task. In experiment 1, we used a 12-element sequence of target positions in space. While
9 the sequence was relatively long, it was not directly related to the sensorimotor adaptation aspect
10 of the task (i.e., force field adaptation). In addition, the presence of four target positions, if not the
11 exact sequence of their presentation, was clear to participants. Therefore, in experiment 2, we used
12 a sequence that was directly related to the force field itself, with a 6-element sequence of force
13 field directions. While subjects were aware of the force field, the slight differences in force field
14 direction were less obvious. Nonetheless, robust sequence learning also occurred in experiment 2.
15 These findings indicate our brain can process sequence learning during sensorimotor adaptation
16 tasks, even when the sequenced elements were subtle and closely integrated with the skill learning.
17 An important consideration for experiment 1 is to what degree the previous reach influenced the
18 current reach. From a dynamics perspective, we might expect such influence to occur, and to
19 potentially cause differences between the sequence and random group at the level of individual
20 reach directions. For example, the reach direction from target 2- target 3 was always preceded by
21 the target 4-target 2 reach for the sequence group. For the random group, the preceding reach
22 varied randomly across epochs, potentially adding variability to the dynamic state of the limb at
23 the beginning of the target 2-target 3 reach. However, in the present task any influence of the

previous reach was likely diminished by requiring subjects to come to a complete halt and wait for a variable period at each target before the next target appeared. This choice of task design simplifies interpretation, but it may be valuable for future studies to eliminate the waiting period to better approximate the complex movement patterns of natural behavior.

4.2 Sensorimotor adaptation occurred under complex force fields

Participants were able to adapt to the force fields in both experiments in the current study. We used a position-dependent force field to mimic the classic velocity-dependent force field characteristics (Shadmehr & Mussa-Ivaldi, 1994). A position-dependent force field provides the same force regardless of the subject's velocity. This was important in the present study because the anticipatory information obtained from sequence learning could potentially increase movement speed (Moisello et al., 2009); had we used a velocity-dependent force field, the sequence group might then have experienced stronger forces than the random group, which would be a confound. While force strength was thus controlled, it is still possible for subjects to experience different impulses (integral of force over time) during adaptation, if they have differences in movement time. However, there was no significant difference between the sequence and random groups in movement time or impulse, for either experiment, suggesting these parameters are unlikely to explain between-group differences in adaptation.

Adaptation to the position-dependent field followed the pattern we would expect with a velocity-dependent field; for both groups in both experiments, the perturbation initially caused large reaching errors that were gradually reduced through trial-and-error practice, with evidence of a negative aftereffect when the force field was abruptly removed (Sexton, Liu, & Block, 2019). This suggests that a position-dependent force field can be used to investigate force field adaptation, even with the interaction of sequence learning.

1 In the first experiment of the current study, there were 12 different reaching directions.
2 Unlike traditional center-out reaching tasks where the starting position of each reach is the same,
3 the start and end position of each reach varied among four different targets on the four corners of
4 a square. This made the task less straightforward to learn as the force field was counterclockwise
5 to the reaching direction. For example, when reaching upward the participant would be pushed to
6 the right by the force field, and when reaching downward the participant would be pushed to the
7 left. Despite the task complexity, we still observed significant adaptation and washout in both
8 sequence and random groups, indicating sensorimotor adaptation occurs robustly under these
9 conditions.

10 The individual reaching directions examined in experiment 1 showed different adaptation
11 magnitudes. Many force field adaptation tasks investigate only one reaching direction (e.g.,
12 forward reaching) (Mawase & Karniel, 2012), or average reaching errors from all directions (e.g.,
13 center-out reaching) (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010). In experiment 1, we
14 covered a wide range of 2-dimensional reach directions. The adaptation and aftereffect curves
15 looked as expected for vertical and diagonal reach directions but were more flat for the horizontal
16 directions. This was the case for both sequence and random with force groups. This might be due
17 to posture and limb dynamics providing greater resistance to perturbation in the lateral reach
18 directions.

19 In the second experiment, the reaching task was simpler in the sense that participants were
20 asked to only reach upward, and the robot would bring their hand back to start position. However,
21 the sequence component was hidden in the force field as the different force directions. All the force
22 directions were rightward with only slight variation in angle, which made it harder to adapt to a
23 changing force field. Though it is a novel type of force field adaptation task (we still used the

position-dependent force field), participants in both groups were able to adapt, indicating the brain was able to learn the changing environment despite multiple force directions.

4.3 Sequence facilitated sensorimotor adaptation

When adding a sequence component to force field adaptation, sequence learning and sensorimotor adaptation both occurred in both experiments. Moreover, we found evidences of sequence learning benefitting adaptation and retention in experiment 2. This could suggest that sequence learning may be more likely to benefit sensorimotor adaptation if the elements being sequenced are the sensorimotor perturbation itself. In contrast, when the sequenced elements were the target positions in experiment 1, the same force field was experienced no matter what target position was presented next, so this sequence could be interpreted as less closely tied to the sensorimotor perturbation. An alternative interpretation might be that the sequence and random groups had more similar levels of predictive information in experiment 1, making between-group differences harder to detect. In other words, the random group in experiment 1 had substantial predictive information because subjects could see each new target position before reaching. In contrast, random group subjects in experiment 2 did not know which force direction would be applied until the reach was underway. If predictive information in general (not just sequence learning) improves force field adaptation, then the experiment 1 random group had an advantage that the experiment 2 random group did not. We cannot say whether other types of predictive information would be as good as, or better than, sequence learning, since we did not directly test other types of predictive information, but this would be an interesting subject for future work.

Aftereffect is an indicator of learning and retention of the force field perturbation that is assessed during the washout block, when force perturbation has been removed. Larger errors in

1 the opposite direction (negative aftereffect) suggest the brain has robustly stored the learned
2 sensorimotor changes (Shadmehr & Mussa-Ivaldi, 1994). A catch reach during adaptation that
3 randomly turn off the perturbation is another way to detect negative aftereffect (Stockinger, Focke,
4 & Stein, 2014). Though we did not find differences in the catch reach or in the washout block
5 between groups in Experiment 1, in Experiment 2 we found significant group effects in both
6 washout blocks. Specifically, the sequence group's negative aftereffect was larger and more
7 persistent (better retained) than the random group.

8 Early adaptation to a force field is substantial and does not differ greatly among typically
9 developing adults (Lamothe et al., 2014; Krakauer & Mazzoni, 2011). We observed similar early
10 adaptation rates between the two groups in experiment 1 as well as the groups in the first adaptation
11 block of experiment 2 when predictive information was not available. However, in the second
12 adaptation block of experiment 2, the sequence group kept the same sequence from the first
13 adaptation block and adapted faster to the external perturbation than the random group. This
14 suggests that the sequence component played an important role in re-learning the sensorimotor
15 perturbation.

16 In Experiment 1, when comparing the perpendicular deviation on an epoch level
17 (averaged every 12 elements), we did not observe group differences. When examining individual
18 reaching directions, there were differences in task performance among some reach directions,
19 indicating the sequence of target appearance might have an influence on some reach directions
20 but not all. In contrast with experiment 1, the sequence component in experiment 2 clearly
21 affected adaptation in the individual force directions. This indicates that this form of sequence
22 component, if added to force field adaptation, might assist the adaptation. Of relevance to
23 Experiment 2, there is evidence that when a force field is variable from trial to trial, subjects

1 learn statistical parameters such as the mean of the perturbation (Scheidt et al., 2001). This was
2 the case when subjects were exposed to a random sequence of velocity-dependent force field
3 magnitudes, perturbing the hand by different magnitudes in the same direction; subjects
4 compensated for the approximate mean of the magnitudes, whether the magnitudes were
5 distributed unimodally or bimodally (Scheidt et al. 2001). A similar process could occur in the
6 present Experiment 2, with subjects learning the average force field direction. However, we do
7 not think this could explain the between-group differences of Experiment 2. Both sequence and
8 random groups experienced force fields with the same statistics; in every epoch of 6 reaches,
9 they experienced the same 6 field directions. Thus, if only the field statistics were being learned,
10 and the presence of a repeating sequence did not matter, we would expect no difference between
11 the groups.

13 **4.4 Implications and future directions**

14 The current study combined two processes that have frequently been studied in isolation.
15 Importantly, we found that sequence learning did not reduce sensorimotor adaptation and was even
16 facilitatory in certain conditions. This has implications for how motor skills should be practiced
17 and taught. For example, whether training an athlete or rehabilitating a stroke survivor, it may be
18 advantageous to encourage repetition of all the elements of the skill in the correct sequence, rather
19 than excessive practice of one element at a time in order to master the sensorimotor aspect first.
20 Further research with more complex sensorimotor demands and more types of sequence will be
21 needed to determine any specific recommendations.

22 Given that sensorimotor and sequence learning are thought to depend on many of the same
23 brain regions, we did consider the alternative that adding sequence learning demands might be

detrimental to sensorimotor adaptation. Specifically, we might have expected that adding a sequence element would exhaust neural resources available for sensorimotor adaptation, leading to reduced adaptation or aftereffect. However, literature directly comparing the two processes is quite limited, and meta analysis of separate neuroimaging studies of the two processes found only that some of the same brain regions such as SMA and premotor cortex are active in both types of study (Hardwick et al., 2013). The present results are inconsistent with the idea that sensorimotor and sequence learning share these neural substrates in any mutually exclusive fashion. The shared brain regions might not serve both processes simultaneously, but instead, gradually shift emphasis from one process to another, or each process might rely on separate populations of neurons within the same brain area.

We did not inform participants about the presence of a sequence. However, many of them noticed some amount of the sequence by the end of the experiment, especially when the sequence was target positions in experiment 1. This shift of implicit learning to explicit learning is common in sequence learning studies (Nissen & Bullemer, 1987). Although researchers have tried to separate explicit and implicit learning in laboratory settings, we do not learn motor behaviors purely relying on only one of them in most of our real-life settings. In the present study, participants perceived the task to be purely a force field reaching task at the beginning. During this early stage of learning, motor areas are highly engaged in learning and understanding the force field (Richardson et al., 2006). As the participants gradually perceived the existence of a sequence to some degree, their reaching performance was already quite improved. At this stage, brain areas such as the SMA and pre-SMA become more involved in the sequence learning aspect of the task (Roland et al., 1980). And when both processes become proficient, fewer neural resources might be required to connect the two processes; indeed, having shared brain regions might have some

benefit. As we observed in the second adaptation block in experiment 2, the re-learning of the force field was more efficient when sequence learning accompanied the previous adaptation block, and retention of force field learning was enhanced after the force field was turned off. This kind of interaction between explicit and implicit learning is supported by the relationship between involved brain areas (Ashe, Lungu, Basford, & Lu, 2006). Supplementary motor area (SMA) and pre-SMA became important during this time. This change of brain area engagement is similar in sensorimotor learning tasks (Hardwick et al., 2013).

The finding of the current study supports the way we often learn in real life scenarios, that learning sequence and sensorimotor aspects together would not impair our learning. However, unlike research settings, in which explicit learning and implicit learning are more strictly separated, people rely on both to learn a sequence in real life. Future research should therefore investigate the effect of explicit sequence learning on sensorimotor adaptation. It is possible that explicit sequence learning could exhaust the sensorimotor resources, especially early in the task when sensorimotor adaptation is also more explicit. When both processes kick in, one might intentionally look for a sequence while trying to adapt to a new environment.

Although we did not find differences in sensorimotor adaptation with sequenced target positions, we cannot rule out target position as a sequence element that might affect sensorimotor adaptation. The sequence of target positions we used in experiment 1 was relatively complex when taking counterclockwise force field and the 12-element-long sequence into account. We might observe differences if we made the targets less distinct from each other, for example, with only slight difference in reach angles. Similarly, based on experiment 2, we cannot conclude that force direction is the only element whose sequencing could facilitate sensorimotor adaptation. Force magnitudes could be another such variable, as it is related to the sensorimotor perturbation itself.

1 Previous studies found participants were not able to adapt to randomly changing force magnitudes
2 (Donchin & Shadmehr, 2002; Mawase & Karniel, 2012), so there may be limitations to this. A
3 systematic study of different combinations of the two is needed.

4 A limitation of the study is lack of “incidental learning”. Many sequence learning tasks
5 implement random catch trials among sequence blocks as a way to study sequence learning
6 (Willingham et al., 1989; Wilkinson & Shanks, 2004). The reaction time or response time, if using
7 a button-press paradigm, would gradually decrease after a few sequence blocks, but a random
8 block would suddenly increase the reaction time or response time. When the previous sequence is
9 resumed, the time would decrease again. This sudden change of time is an indicator of sequence
10 learning. In the current study, we did not add such a random epoch into the force field adaptation
11 task, which limited us to comparing reaction time early and late in the session to evaluate sequence
12 learning. However, we chose not to add such random epochs due to the task complexity. If random
13 epochs were added into adaptation blocks, reaching error would likely increase for the sequence
14 groups, making it difficult to compare adaptation between groups. Moreover, the number of
15 reaches in the adaptation blocks would have had to increase to ensure the same opportunity for
16 sequence learning as the random group, but then the sequence group would have longer force field
17 exposure. In other words, we chose not to add a random epoch to avoid unnecessarily complicating
18 the interpretation. But with the findings from the current study that sequence learning did not
19 impair force field adaptation, future studies could add random epochs to an easier sensorimotor
20 task to better investigate the role of sequence learning on sensorimotor adaptation.

21 Another aspect of sequence learning that should be considered in future work is
22 “chunking”. In classic sequence learning paradigms such as the SRTT, small groupings of
23 sequence elements are thought to be chunked into sub-sequences. This is detected as increased

reaction time between chunks relative to within chunks, and is thought to improve performance and computationally simplify representation of the sequence (Sakai et al., 2003). In addition to button pressing tasks, the concept of chunking has been applied to compound reaching trajectories. Ramkumar et al. (2016) suggested that chunking is an efficient and cost-effective strategy for learning compound movements. The authors found that monkeys learned sequences of center-out reaches by chunking, which was indicated by locally-optimized trajectories within chunks. In other words, without chunking, the animal would come to a halt at each target in the sequence. As chunking gradually developed, the arm would pass through targets within a chunk without halting, but be more likely to halt between chunks (Ramkumar et al., 2016). Movement within a chunk would thus be smoother. The task design of the present study unfortunately prevents us from analyzing sequence learning this way; subjects were required to halt at each target for a variable delay before the next target appeared. However, studying kinematically-defined chunks could be an important avenue for translating sequence learning principles to sensorimotor adaptation paradigms, and eventually, to applications such as motor rehabilitation.

5. Conclusion

The current study investigated the effect of adding sequence learning to a sensorimotor adaptation task in two different sequence paradigms. When the sequence was target positions in space, sequence learning did not influence the force field adaptation. However, when the sequence was force directions, adding the predictive information improved both retention and the rate of re-learning. Our findings indicate these two processes, when learnt together, are unlikely to monopolize each other's neural resources, and might in turn facilitate each other in some conditions.

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Figure 1. A. i. KINARM End-Point apparatus setup. Participants grasped the manipulandum and viewed tasks from the mirror. **ii.** Schematic of the position-dependent forces applied at each point along the path from one target to the next. The force magnitude vectors are perpendicular to the straight line connecting the two targets, which represents the forces applied in Experiment 1, as well as the horizontal-direction forces in Experiment 2. **B.** Experiment 1 study design. **i.** Task layout for a right-handed participant. T1-4: labels for the four target positions. Red target was the start position for each epoch of 12 reaches. **ii.** Task blocks for sequence targets with force field group and example movement paths of a participant's first epoch in each block. **C.** Experiment 2 study design. **i.** Task layout for a right-handed participant. Red target was the start position for each reach. F1 was the perpendicular force direction; F2 was the 45° force direction; F3 was the 315° force direction. **ii.** Task blocks for sequence directions with force field group and example movement paths of a participant's first reach in each block.

Figure 2. Experiment 1 group results. **A.** Normalized group mean sensorimotor errors across epochs, with each epoch consisting of 12 reaches. Maximum perpendicular error in each epoch, averaged across directions and normalized to baseline. Epoch 1-25: adaptation block. Epoch 26-35: washout block. Dotted line indicated the epoch that had the catch reach. Inset: group average fit line to reaches 2-11 (within epoch 1); slope represents early adaptation rate. **B.** Movement time across adaptation epochs. **C.** Force impulse across epochs of the adaptation block. **D.** Early adaptation rate. **E.** Reaction time (RT) in the first epoch of adaptation and last epoch of washout. * Significant time x group interaction ($p < 0.01$), suggesting RT decreased in the sequence group relative to the random group. Error bars and shading: 95% confidence interval.

Figure 3. Normalized group adaptation curves for the 12 individual reach directions in an epoch. Epoch number 1-25: adaptation block. Epoch number 26-35: washout block. **A.** Vertical reaches. Dotted line in reach direction 5 indicates the catch reach. **B.** Diagonal reaches. **C.** Horizontal reaches. G: statistically significant main effect of group in the adaptation or washout blocks. I: statistically significant interaction of group and time in the adaptation or washout blocks. Error bars: 95% confidence interval. * $p < 0.05$. ** $p < 0.01$.

Figure 4. Experiment 2 group results. **A.** Group mean sensorimotor errors across epochs, with each epoch consisting of 6 reaches. Maximum perpendicular deviation was normalized to baseline. Epoch number 1-30: adaptation 1. Epoch 31-37: washout 1. Epoch 38-52: adaptation 2. Epoch 53-56: washout 2. G: statistically significant main effect of group in the adaptation or washout blocks. I: statistically significant interaction of group and time in the adaptation or washout blocks. Insets: group average fit line to reaches 2-11 (within epochs 1 and 2), with slope representing early adaptation rate. **B.** Early adaptation rate, taken from reaches 2-11 in the first two epochs of adaptation. ** $p < 0.01$. **C.** Reaction time in the first and last epoch of sequence learning. * Significant time x group interaction ($p < 0.05$), suggesting RT decreased in the sequence relative to random group. Error bars and shading: 95% confidence interval.

Figure 5. Adaptation curve for each force direction. For each force direction, every two reaches (1 epoch) were averaged. **A.** 0° force direction. **B.** 45° force direction. **C.** 335° force direction. **i.** Adaptation 1. **ii.** Adaptation 2. G: statistically significant main effect of group in the adaptation blocks. I: statistically significant interaction of group and time in the adaptation blocks. Shading: 95% confidence interval. * $p < 0.01$.

Figure 1

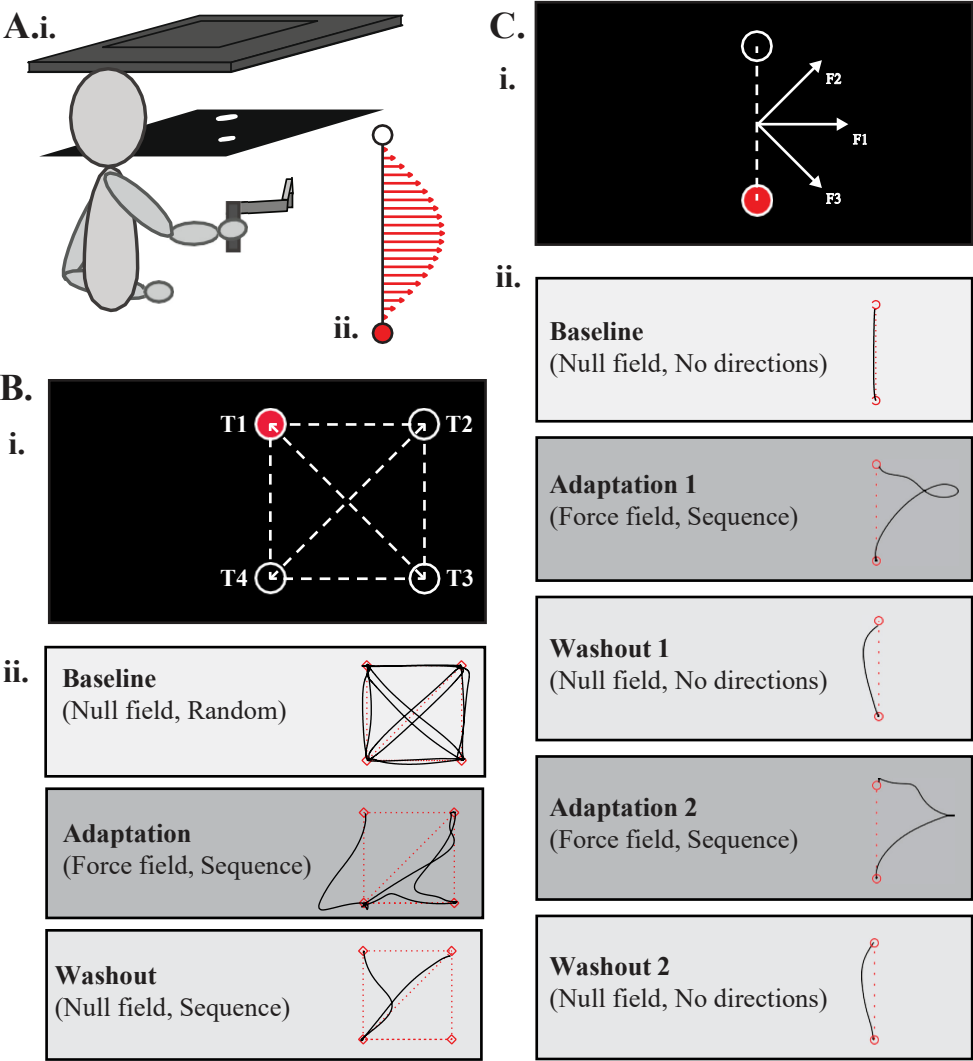


Figure 2

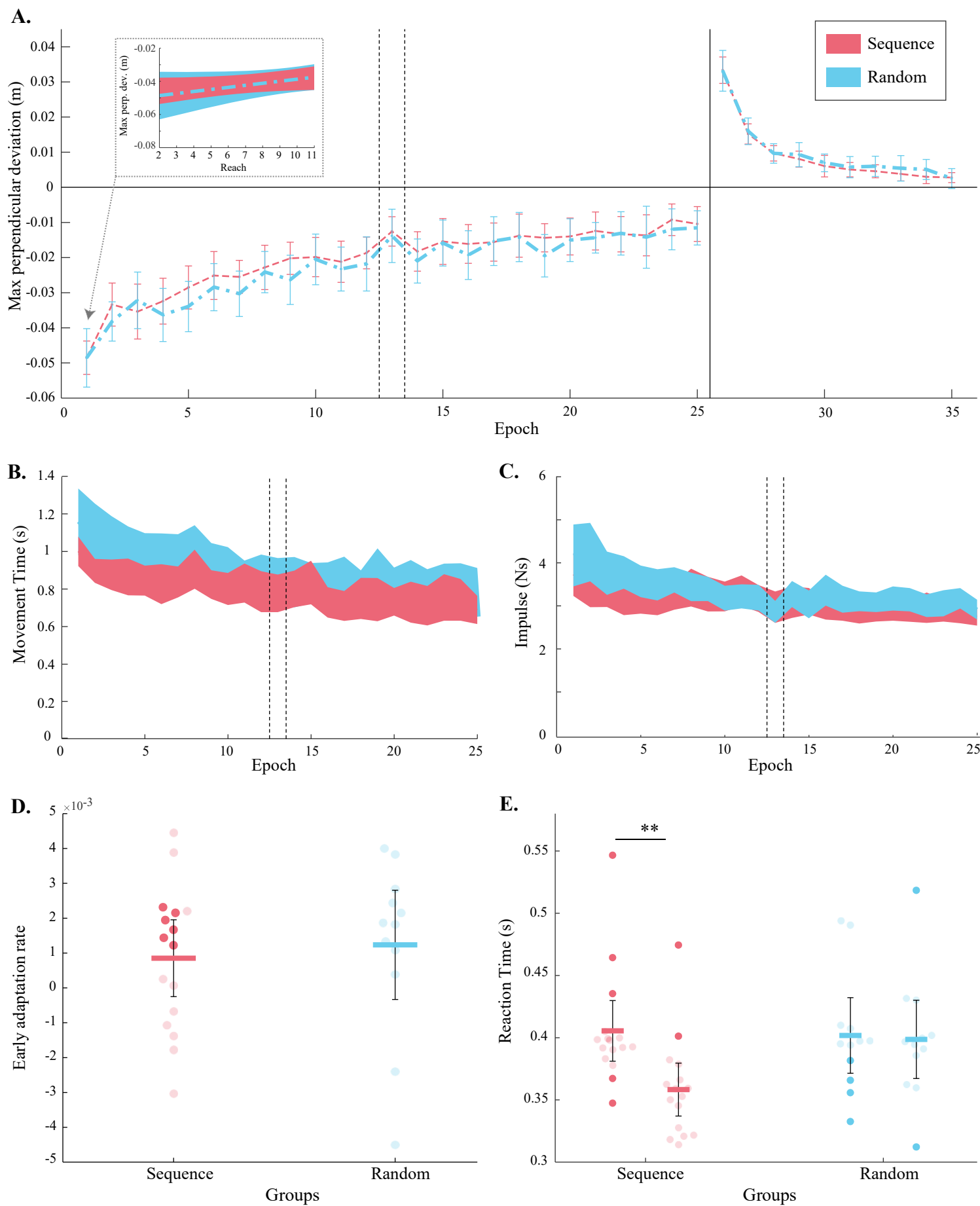


Figure 3

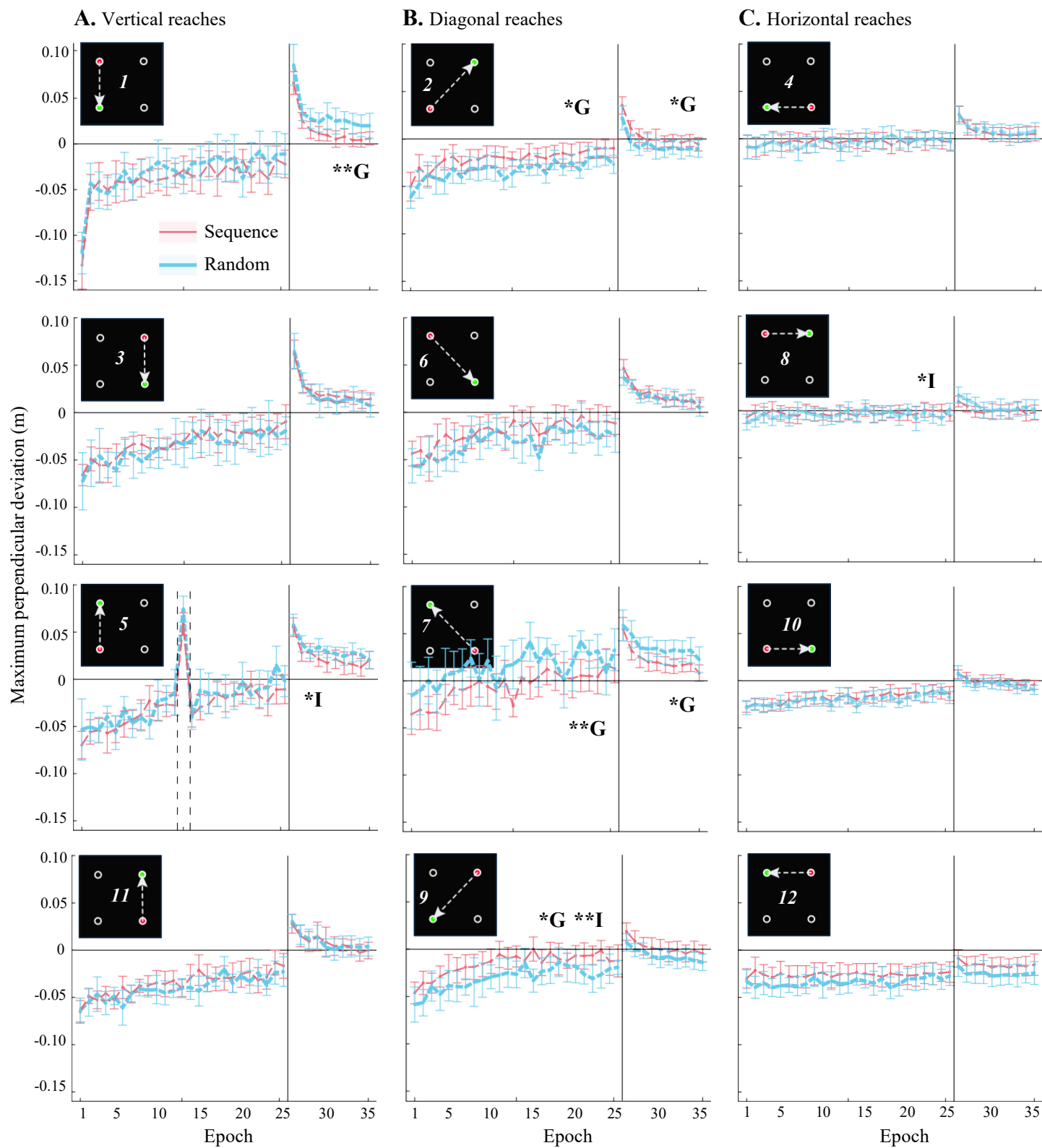


Figure 4

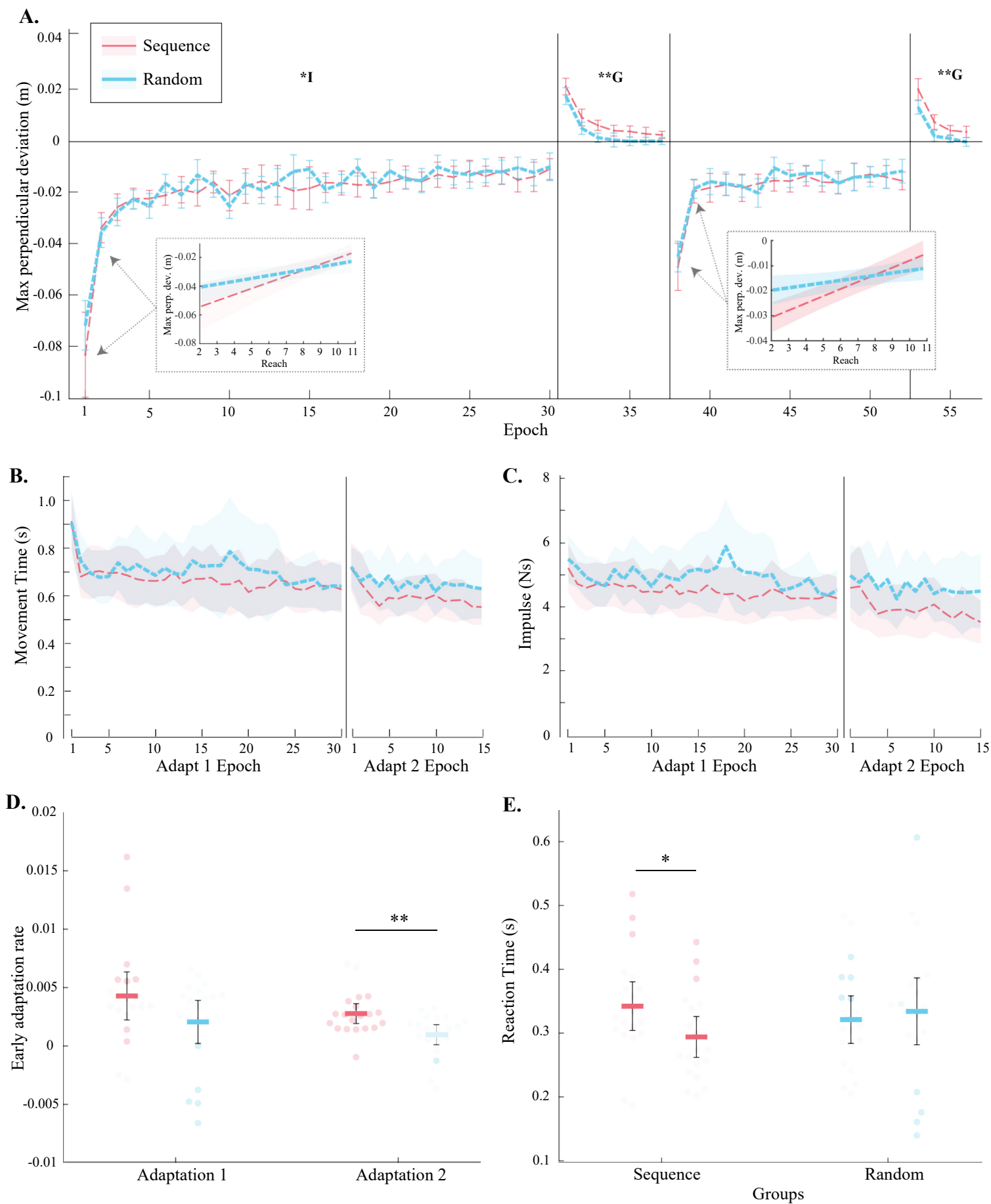
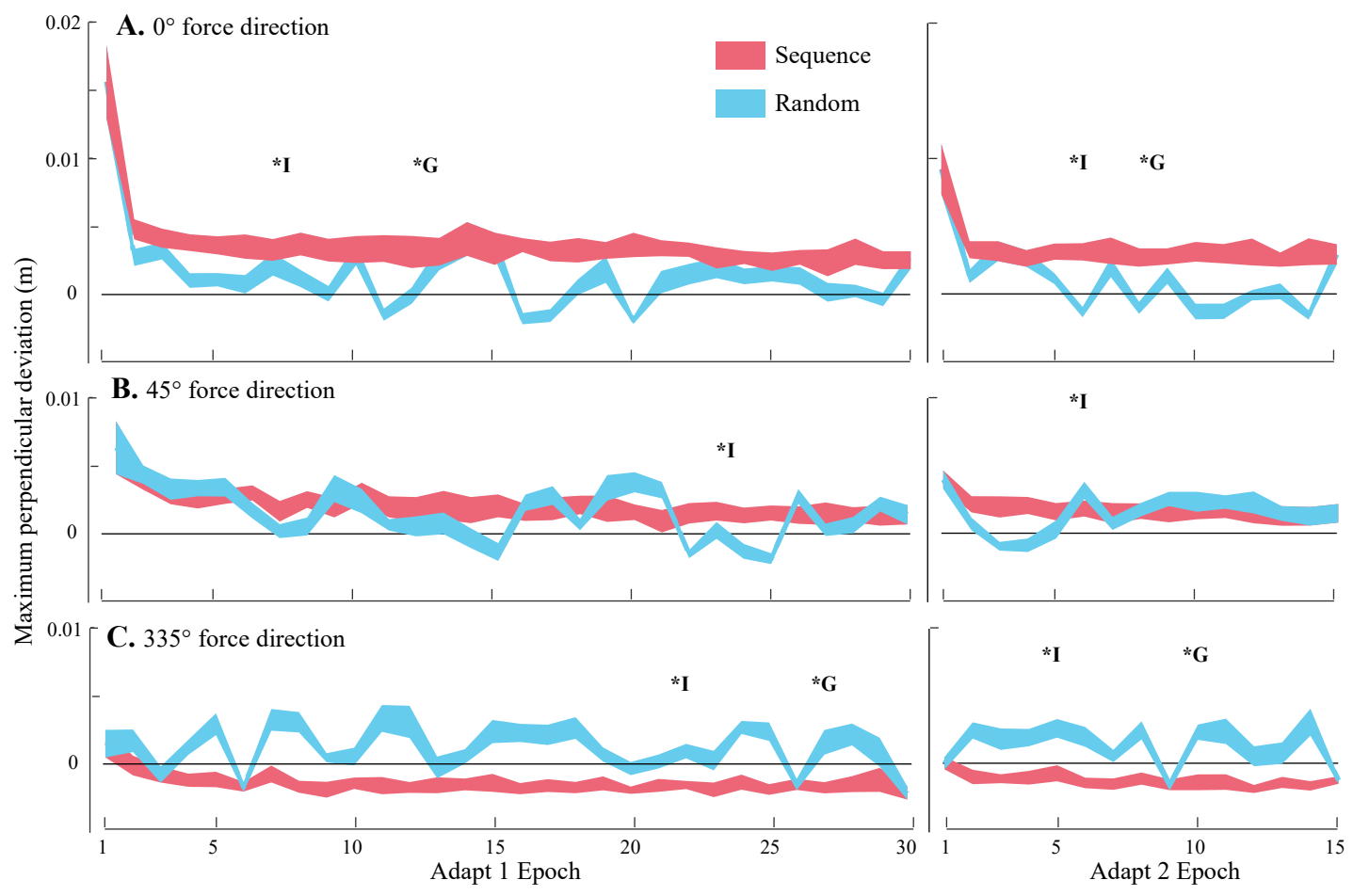


Figure 5



YL: Conceptualization, Methodology, Data collection, Data analysis, Writing – original draft.

HJB: Conceptualization, Data analysis, Writing – review \& editing, Supervision.