INTERFERENCE BETWEEN COMPETING MOTOR MEMORIES DEVELOPED THROUGH LEARNING WITH DIFFERENT LIMBS

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RUNNING HEAD: Motor memories developed with different limbs interfere

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ABSTRACT

Learning from motor errors that occur across different limbs is essential for effective tool use, sports training and rehabilitation. To probe the neural organization of error-driven learning across limbs, we asked whether learning opposing visuomotor mappings with the two arms would interfere. Young right-handers first adapted to opposite visuomotor rotations A and B with different arms, and were then re-exposed to A 24 hours later. We observed that re-learning of A was never faster, nor were initial errors smaller than prior A learning, which would be expected if there was no interference from B. Rather, errors were greater than or similar to, and learning rate was slower than or comparable to previous A learning depending on the order in which the arms learned. This indicated robust interference between the motor memories of A and B when they were learned with different arms in close succession. We then proceeded to uncover that the order-dependent asymmetry in performance upon re-exposure resulted from asymmetric transfer of learning from the left arm to the right but not vice-versa, and that the observed interference was retrograde in nature. Such retrograde interference likely occurs because the two arms require the same neural resources for learning, a suggestion consistent with that of our past work showing impaired learning following left inferior parietal damage regardless of the arm used. These results thus point to a common neural basis for formation of new motor memories with different limbs, and hold significant implications for how newly formed motor memories interact.

NEW AND NOTEWORTHY

In a series of experiments, we demonstrate robust retrograde interference between competing motor memories developed through error-based learning with different arms. These results provide evidence for shared neural resources for the acquisition of motor memories across different limbs, and also suggest that practice with two effectors in close succession may not be a sound approach in either sports or rehabilitation. Such training may not allow newly acquired motor memories to be stabilized.

KEYWORDS

Motor learning, visuomotor adaptation, generalization, retrograde interference, interlimb transfer

INTRODUCTION

Understanding the mechanisms and neural organization of motor learning has been a long-standing pursuit in motor neuroscience, particularly because it is thought to have implications for movement rehabilitation following neurological injury. Motor learning has been studied largely in the context of motor adaptation, which requires learning to adjust motor output to compensate for the effects of novel but predictable visuomotor or dynamic perturbations. Studies on adaptation have revealed that it is driven by a variety of processes, including development of a new internal model or representation of the relationship between movement and its sensory consequences (Gandolfo et al. 1996; Imamizu et al. 1995; Sainburg et al. 1999; Shadmehr and Mussa-Ivaldi 1994; Wang and Sainburg 2005), explicit learning strategies (Heuer and Hegele 2008; 2011; Taylor et al. 2014), and operant mechanisms (Classen et al. 1998; Diedrichsen et al. 2010; Huang et al. 2011; Verstynen and Sabes 2011).

Further insight about these mechanisms that mediate learning and the nature of the resulting motor memories can be obtained by examining how it generalizes to unpracticed conditions, a principle that in fact applies to multiple learning systems such as the declarative (Alvarez and Squire 1994) and perceptual (Yotsumoto et al. 2009) systems . Some studies on motor memory generalization have revealed that the memories developed via motor adaptation comprise of both effector-dependent and effector-independent components (Wang and Lei 2015; Wang et al. 2015). Effector-independence has been surmised from the finding that learning with one effector often generalizes to another, untrained effector. However, there is tremendous heterogeneity in findings of transfer: it depends on a variety of factors including, but not limited to, handedness, movement kinematics and the perceived source of errors (Lefumat et al. 2015). Further, transfer is often variable in magnitude (Joiner et al. 2013; Wang et al. 2015), asymmetric (Criscimagna-Hemminger et al. 2003; Wang and Sainburg 2004a), may be influenced by coordinate frames in which learning occurs (Carroll et al. 2014; Poh et al. 2016), and may not even occur at all (Bock et al. 2005). Such diversity in findings on inter-effector transfer makes clear interpretations about the effector-independence of the motor memories quite challenging.

An alternative approach to understand effector independence of motor memories may be to examine whether and how motor memories developed through learning with different limbs interfere. Interference occurs when two opposing visuomotor mappings or force perturbations (say A and B) are learned in close succession (Brashers-Krug et al. 1996; Goedert and Willingham 2002; Krakauer et al. 1999; Miall et al. 2004). The memory for A is generally examined 24 hours after it is initially learned. If upon re-exposure, errors during the initial trials are smaller and/or A is relearned faster than naïve A learning, it is thought that the intervening learning of B did not interfere with the memory of A. In contrast, similar or greater errors on re-exposure, or re-learning at a slower or even comparable rate, are indicators that the learning of B interfered with the memory of A. Interference presumably occurs because A and B compete for the same neural resources during learning, which is actually not surprising because

A and B are often of the same type and the same arm is used to learn both (Wigmore et al. 2002). It has been proposed that in order to prevent interference, A and B must be associated with distinct movement contexts, which presumably sets different neural states during learning, and allows A and B to be learned and remembered simultaneously (Cothros et al. 2009; Hirashima and Nozaki 2012; Howard et al. 2013; Nozaki et al. 2006; Sheahan et al. 2016).

This interference paradigm, although very attractive, has surprisingly not been fully exploited to understand learning across different effectors and interlimb interactions following such learning. The few studies that have examined whether opposing perturbations can be learned if they are associated with different limbs have largely shown no interference between the memories developed as a consequence of learning (Bock et al. 2005; Galea and Miall 2006). This may be because use of the two limbs involves distinct sensorimotor transformations, which may be mediated by activation in distinct neuronal populations. As stated earlier, these differences in activity patterns could provide distinct contextual cues during learning, thereby allowing opposing perturbations to be learned. However, if motor memories developed through such learning comprise of effector-independent components as suggested by studies on transfer, interference should be evident. Here we attempted to reconcile these contradictory positions and investigated whether competing motor memories developed through adaptation to two opposing visuomotor mappings with different arms would interfere. In a series of experiments, we found robust interference between these newly formed motor memories. We also noted that this interference is retrograde in nature, and likely occurs because a new memory developed through learning with one arm erases a prior memory developed with the other. Such interference holds significant implications for how newly formed motor memories interact.

MATERIALS AND METHODS

Subjects

A total of 48 young, healthy, right-handed individuals (39 men, 9 women, age range: 20–30 years) participated in the study. Handedness was assessed using the Edinburgh handedness inventory (Oldfield 1971). Subjects did not report any neurological disorders, cognitive impairment or orthopedic injuries. All subjects provided written informed consent prior to participation and were paid for their time. The study was approved by the Institute Ethics Committee of the Indian Institute of Technology Gandhinagar.

Apparatus

The experimental setup comprised of a virtual realty system in which subjects sat facing a large, horizontally placed digitizing tablet (Calcomp Inc.) and used a stylus to make planar movements on it (Fig. 1A). The position of the hand (stylus) was represented as a cursor on a horizontally mounted HDTV placed above the tablet. A circular start position and circular targets were also displayed. A mirror was placed between the TV screen and the arms to reflect the projected display and to block vision of the arm itself. The position of the cursor could either be veridical or distorted relative to the motion of the hand.

Task Procedure

After familiarization with the setup and a few practice movements, subjects performed 13 cm long reaching movements from a central start circle (1.5 cm diameter) to eight radially arranged targets (2.5 cm diameter), spaced 45 degrees apart from each other. To initiate a trial, subjects first brought the cursor into the start circle, and stayed in it for 500 ms to get one of the eight targets along with an audiovisual “go” cue. The order of target presentation was decided pseudorandomly before the experiment such that each target appeared only once over eight consecutive trials (one cycle) and there was no sequential presentation of the set of eight targets. This order was then kept the same for all subjects and experimental conditions. Thus all subjects made movements to the same target on any “i^{th}” trial. Subjects were instructed to make fast and accurate movements to a displayed target; numerical points were given based on movement accuracy. If the movement ended within the target, 10 points were given; if it ended outside the target but within 2.5 cm from the edge of the target, 5 points were given. No points were given if the end point of the movement was beyond this distance. Points did not influence the payment the subject received at the end of the experiment; points were also not analyzed.

Experiment 1: In our first experiment, subjects were required to adapt their movements to a new mapping (visuomotor rotation) between hand motion and its visual feedback (on-screen cursor). Subjects were divided into four groups. Subjects in Group 1 (n=8, Fig. 1B, top-left panel) first adapted a 30° clockwise rotation by performing 256 trials with their right arm ($CW_{R,1}$), followed by adaptation to a 30° counterclockwise rotation with the left arm (256 trials, $CCW_{L,1}$). The same start position and targets were used for both arms, subjects made 32 movements to each target, and the rotation was applied on all 256 trials. Subjects were then re-exposed to the clockwise rotation 24 hours later and were required to adapt to it using their right arm ($CW_{R,2}$). Subjects again performed 256 trials. The signature of interference in Group 1 would be either greater or even similar errors initially, and/or a slower or even similar learning rate during $CW_{R,2}$ compared to $CW_{R,1}$. However, this comparison alone is not enough, since it must also be shown that initial $CW_{R,2}$ errors are smaller or learning is faster than $CW_{R,1}$ learning in a group that does not learn the intervening $CCW_{L,1}$. We therefore included a control group (n=8, Group 2, Fig. 1B, top-right panel) that performed the same task, but did not undergo left arm adaptation. Thus, they learned $CW_{R,1}$ and were directly exposed to $CW_{R,2}$ 24 hours later (256 trials in each session). A separate group of subjects (n=8, Group 3, Fig. 1B, middle-left panel) did the task in the reverse order. These subjects first adapted over 256 trials to the 30° clockwise rotation with the left arm ($CW_{L,1}$), followed by adaptation to a 30° counterclockwise rotation with the right arm ($CCW_{R,1}$) thereafter (256 trials). They were then re-exposed with their left arm (256 trials) to the clockwise rotation 24 hours later ($CW_{L,2}$), and their performance was compared to another control group (n=8, Group 4, middle-right panel) that simply practiced $CW_{L,1}$ and was re-exposed to the same rotation after 24 hours ($CW_{L,2}$) without any intervening $CCW_{R,1}$ learning. Again, interference would be reflected as similar or larger errors initially, and/or a similar or slower learning rate during $CW_{L,2}$ compared to $CW_{L,1}$ for Group 3.

Experiment 2: In Experiment 1, clear interference between the memories developed from learning the opposing rotations was seen for Groups 1 and 3. To better understand the nature of this interference, we performed a second experiment in which subjects (n=8, Group 5, Fig. 1B, bottom-left panel) performed 64 null (no rotation) trials before each exposure to the rotation. The arm that was used during the null trials was the same as that used for subsequent adaptation. The start and target locations were identical to Experiment 1. Additionally, because we had already demonstrated interference regardless of the order in which the arms were used in Experiment 1, this second experiment was done only in the right-left-right arm order. Thus, subjects first performed 64 $N_{R,1}$ trials, followed by 256 $CW_{R,1}$ trials, and then performed 64 $N_{L,1}$ trials followed 256 $CCW_{L,1}$ trials. 24 hours later, they began with a block of 64 $N_{R,2}$ trials followed by 256 trials of $CW_{R,2}$ learning. In sum, we followed a $N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CW_{R,2}$ task design.

Experiment 3: Interference between the $CW_{R,1}$ and $CCW_{L,1}$ memories was still evident in Experiment 2. We undertook a third experiment to validate whether this interference was retrograde in nature. Our Experiment 3 was identical to Experiment 2 in all respects except that the time duration between $CW_{R,1}$ and the subsequent $N_{L,1}CCW_{L,1}$ blocks of trials was increased to 24 hours. As in Experiment 2, subjects (n=8, Group 6) were re-tested on the $N_{R,2}CW_{R,2}$ trials 24 hours after their $CCW_{L,1}$ learning (Fig. 1B bottom-right panel). Thus, we still followed a $N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CW_{R,2}$ paradigm, but with a 24 hour gap between the initial adaptation episodes (i.e. between $CW_{R,1}$ and $CCW_{L,1}$). We expected that if the interference between these memories is indeed retrograde, increasing the time duration between their initial learning experiences would lead to a reduction in interference, a classic signature of a retrograde process.

Data Analysis

Kinematic data were filtered using a low-pass Butterworth filter with a cutoff frequency of 10 Hz. Position data were differentiated to provide velocity values. Adaptation to the rotation was quantified as a reduction in movement direction error across trials; these errors were calculated as the angle between the line connecting the start position and the target, and the line connecting the start position and hand position at peak tangential velocity. The rate of adaptation was quantified by robust fitting a single-rate exponential function of the form

$$(y = C * exp^{-\beta * x}) \qquad \text{[Equation 1]}$$

to the direction error data, where y represents the error, C is a constant, x represents trial number and β is the learning rate. Both, the constant C and the learning rate were estimated separately for each subject in each condition. The details of the statistical tests used for comparing the different groups are provided along with the corresponding results. Effect sizes are reported as Cohen's d_z or Cohen's d_s for paired and unpaired comparisons respectively (Lakens 2013). The significance threshold for all comparisons was set at 0.05.

RESULTS

Experiment 1: Opposing motor memories developed with the two limbs interfere

In Experiment 1, subjects in Group 1 adapted in a $CW_{R,1}$-$CCW_{L,1}$-$CW_{R,2}$ order. All these subjects showed canonical learning patterns for the $CW_{R,1}$ block: their movement trajectories were curved upon initial exposure to the rotation (Fig. 2A, thick red) and gradually became straighter (Fig. 2B, thin red), which was also reflected as a reduction in initial direction errors with practice (Fig. 2E, red). $CCW_{L,1}$ learning appeared similar to $CW_{R,1}$ learning with curved trajectories initially (Fig. 2C), straightening of these trajectories over time (Fig. 2D) and a gradual reduction of motor errors with practice (Fig. 2E, green). Learning rates (Table 1) were not significantly different for the two arms (paired t-test, $t_{(7)}=0.46$, $p=0.66$, 95%CI=[-0.017,0.026], Cohen's $d_z=0.162$; Fig. 2F).

When Group 1 subjects were re-exposed to the clockwise rotation 24 hours later their early $CW_{R,2}$ trajectories were more deviated (Fig. 2A, thick blue), and they showed larger errors on the first trial (Table 2) compared to $CW_{R,1}$ learning. In contrast, control subjects (Group 2) who did not undergo any left arm $CCW_{L,1}$ training between $CW_{R,1}$ and $CW_{R,2}$ showed substantial retention of the $CW_{R,1}$ memory. These subjects showed less deviated trajectories during the early $CW_{R,2}$ trials (Fig. 2G, compare thick blue to thick red), which then also quickly straightened (Figure 2H, thin blue). Averaging across subjects in Group 2, the $CW_{R,2}$ errors appeared smaller on the initial trials (Table 2, Fig 2I, blue versus red profiles).

Statistical confirmation of these results was obtained via a two-way ANOVA with group (Group 1, Group 2) and learning block ($CW_{R,1}$, $CW_{R,2}$) as factors. The ANOVA revealed a significant interaction effect for the direction error on the first trial ($F_{(1,14)}$=17.05, p=0.0010). Tukey's post-hoc tests confirmed that while the errors in the $CW_{R,1}$ block were not different between the groups (p=0.6344, Table 2), errors in the $CW_{R,2}$ block were far greater for Group 1 (the group that also practiced $CCW_{L,1}$) than Group 2 (p=0.0019, Table 2). Importantly, $CW_{R,2}$ errors for subjects in Group 1 were also greater than their own $CW_{R,1}$ errors (p=0.04, Table 2). There was also main effect of group ($F_{(1,14)}$=6.97, p=0.02), but the main effect of learning block was not significant ($F_{(1,14)}$=0.0001, p=0.99). Subjects in Group 1 also adapted more slowly during the $CW_{R,2}$ block than $CW_{R,1}$ learning (paired t-test, $t_{(7)}$=2.53, p=0.039, 95%CI=[0.001,0.02], Cohen's d_z=0.9; Fig. 2C, Table 1). Such a decrement in $CW_{R,2}$ learning in Group 1 reflected interference between the $CW_{R,1}$ and $CCW_{L,1}$ memories developed with through learning with the two arms.

Interference was also evident for subjects in Group 3, who used the two arms in the reverse order ($CW_{L,1}$-$CCW_{R,1}$-$CW_{L,2}$). In this group, left arm $CW_{L,1}$ trajectories were curved upon initial exposure to the rotation (Fig. 3A, thick red), but became straighter with practice (Fig. 3B, thin red). Direction errors also decreased over time as expected (Fig. 3E, red). When the right arm was subsequently exposed to the counterclockwise rotation ($CCW_{R,1}$), errors on the first trial were significantly greater than 30 degrees ($t_{(7)}$=7.05, p<0.001, 95%CI=[42.42,54.944], Table 2, Fig. 3C), but became close to zero over time

(Fig. 3D and 3E, green). This reduction in error was slower compared to prior $CW_{L,1}$ learning (paired t-test, $t_{(7)}$=3.48, p=0.01, 95%CI=[0.002,0.012], Cohen's d_z=1.23, Table 1, Fig. 3F) as well as naïve $CW_{R,1}$ learning of Group 1 (unpaired t-test, $t_{(14)}$=-3.39, p=0.004, 95%CI=[-0.022,-0.005], Cohen's d_s=1.3). When the left arm was re-exposed to the clockwise rotation 24 hours later ($CW_{L,2}$), we found that subjects in Group 3 did not show larger errors on the initial trials as was the case for $CW_{R,2}$ learning of Group 1 (see Table 2 for mean values). The overall learning pattern also did not appear to be very distinct from $CW_{L,1}$ learning. Left arm trajectories on the early and late rotation trials of the two sessions largely overlapped (compare red and blue trajectories of Figs. 3A and 3B), as did the learning curves (compare red and blue profiles in Fig. 3E). This was in contrast to another control group (Group 4) which did not learn $CCW_{R,1}$ between the $CW_{L,1}$ and $CW_{L,2}$ sessions. Like Group 2, subjects in Group 4 showed retention of prior learning when they were re-exposed to the rotation: their trajectories appeared less deviated (Fig. 3G, compared thick blue profiles to thick red trajectories) and became straight with continued exposure (Fig. 3H). These subjects had smaller errors on the initial trials during $CW_{L,2}$ learning compared to $CW_{L,1}$ (Table 2, Fig. 3I).

These trends were statistically confirmed by means of an ANOVA that included group (Group 3, Group 4) and learning block ($CW_{L,1}$, $CW_{L,2}$) as factors. We observed significant main effects for both group ($F_{(1,14)}$=6.13, p=0.03) and learning block ($F_{(1,14)}$=9.24, p=0.01). More importantly however, there was also a significant group X learning block interaction ($F_{(1,14)}$=6.85, p=0.0202), with post-hoc tests revealing that while errors on the first trial were smaller in $CW_{L,2}$ compared to $CW_{L,1}$ for Group 4 (p=0.0063, Table 2), there was no difference between the initial $CW_{L,2}$ and $CW_{L,1}$ errors for Group 3 (p=0.9903, Table 2). Furthermore, there was no significant difference in the learning rate during the $CW_{L,1}$ and $CW_{L,2}$ blocks for the subjects in Group 3 (paired t-test, $t_{(7)}=-0.65$, p=0.53, 95%CI=[-0.008,0.005], Cohen's $d_z=0.23$; Fig. 3F). Given the strong retention of the $CW_{L,1}$ memory in the group that did not practice $CCW_{R,1}$ (Group 4), the overlap seen in Group 3 cannot be attributed to some default inability to retain left arm learning. Rather, this is a signature of interference from the prior $CCW_{R,1}$ memory. To summarize, in Experiment 1, we noted that 1) the right arm always showed larger errors initially and learned more slowly when it followed left arm adaptation but not vice-versa, and 2) the learning of opposing mappings with the two limbs in close succession led to substantial interference between the two motor memories.

Experiment 2: Interference persists despite removal of anterograde effects

We posited that these effects could arise due to a combination of factors: 1) inter-effector transfer of learning: the decrement in performance with the right arm following left arm adaptation could occur because aftereffects of left arm training persist and transfer to the right arm (but not vice-versa), 2) anterograde interference: the observed interference between the two motor memories could occur because a memory developed after learning with one arm blocks subsequent learning with a different arm giving rise to interference, and/or 3) retrograde interference: the interference could occur because a newly formed memory erases a prior memory developed with the other arm or blocks its retrieval. To distinguish between these, in a new experiment (Experiment 2), we exposed a new set of subjects (Group 5) to null (no rotation, N) trials before each learning episode. For simplicity, and also because we had established the directionality of the effects in Experiment 1, we restricted this second experiment to only a right-left-right arm order ($N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CW_{R,2}$ design, Fig. 1B, bottom-left panel). We reasoned that the initial exposure to null trials in $N_{R,2}$ would unmask any transfer of aftereffects from the left arm to the right, and this would be evident as large errors on these trials despite the absence of a rotation. We further surmised that subsequent practice on these null trials would washout anterograde effects and allow the expression of any memory that was potentially still intact. If this were indeed the case, $CW_{R,2}$ learning would be faster than that seen in the $CW_{R,1}$ block. However, the same or slower learning rate during $CW_{R,2}$ would indicate that interference still occurred between the two motor memories.

We first noted that $N_{R,1}$ and $CW_{R,1}$ trajectories for subjects in Group 5 were as expected. Null movements were smooth and directed straight towards the target initially (Fig. 4A, thick red) and continued to be as such towards the end of the null block (Fig. 4B, thin red). $CW_{R,1}$ trials showed large curvature initially because of the rotation (Fig. 4C, thick red), but became straighter with practice (Fig. 4D, thin red). Direction errors on null trials were close to zero (Table 2) and subsequently, subjects showed the typical learning curve with errors starting close to 30 degrees and decreasing with practice (Fig. 4I, red). Early $N_{L,1}$ hand trajectories of subjects in this group were also straight (Fig. 4E) and errors were close to zero (Table 2). This continued to be the case even at the end of the $N_{L,1}$ block (Figs. 4H). The $CCW_{L,1}$ handpaths for these subjects (Figs. 4G and 4H) and learning curve (Fig. 4I, green) did not appear to be different from that seen in Group 1 of Experiment 1. In fact, a comparison of learning rates (Table 1) for $CCW_{L,1}$ of Group 5 and $CCW_{L,1}$ of Group 1 revealed no significant differences (unpaired t-test, $t_{(14)}=1.16$, $p=0.26$, 95%CI=[-0.007,0.025], Cohen's $d_s=0.57$).

Interestingly, in Group 5, $N_{R,2}$ performance 24 hours later showed clear evidence of transfer of aftereffects from $CCW_{L,1}$ learning. Right arm trajectories on the initial $N_{R,2}$ trials were substantially curved even though no rotation was applied (Fig. 4A, thick blue) and notably, the curvature was in the direction of trained $CCW_{L,1}$ hand movements. Errors on the first $N_{R,2}$ trial were greater compared to $N_{R,1}$ trials (paired t-test, $t_{(7)}=6.67$, $p<0.0003$, 95%CI=[15.626,32.797], Cohen's $d_z=2.35$, Table 2), indicating robust transfer of after-effects from the left arm to the right. Interestingly, the magnitude of these errors in Group 5 was not significantly different than the decrement (difference between errors on the first $CW_{R,2}$ and $CW_{R,1}$ trials) seen on the first trial for Group 1 in Experiment 1 (unpaired t-test, $t_{(14)}=-1.54$, $p=0.147$, 95%CI=[-15.67,2.58], Cohen's $d_s=0.73$). Subsequent $N_{R,2}$ practice washed out the after-effects for the Group 5 subjects, their handpaths became straight (Fig. 4B, thin blue) and the direction errors became close to zero towards the end of the $N_{R,2}$ block. We then noted that the ensuing $CW_{R,2}$ learning was not different from $CW_{R,1}$; the learning curves overlapped (compare red and blue learning curves in

Fig. 4I), and neither the errors on the first learning trial (paired t-test, $t_{(7)}$=-1.15, p=0.287, 95%CI=[-9.25,3.19], Cohen's d_z=0.4; Fig. 4I, Table 2) nor the learning rate (paired t-test, $t_{(7)}$=-0.04, p=0.967, 95%CI=[-0.007,0.006], Cohen's d_z=0.01, Table 1, Fig 4J) were significantly different. This indicated that interference continued to occur in Group 5 despite the removal of after-effects and washout of anterograde influences, and might therefore be retrograde in nature.

Experiment 3: Interference is retrograde in nature

If the interference is indeed retrograde, then increasing the time between the initial learning episodes should lead to a reduction in interference. We confirmed this in Experiment 3, in which participants (Group 6) learned $CW_{R,1}$ and $CCW_{L,1}$ 24 hours apart, and were then tested on $CW_{R,2}$ 24 hours after $CCW_{L,1}$ learning. We first noted that null performance as well as $CW_{R,1}$ and $CCW_{L,1}$ learning in these subjects (Group 6) appeared similar to Experiment 2 (Fig. 5A-H). There was no difference in learning rate between Groups 5 and 6 for either $CW_{R,1}$ (unpaired t-test, $t_{(14)}$=-1.10,p=0.29, 95%CI=[-0.01,0.003], Cohen's d_s=0.54) or $CCW_{L,1}$ learning (unpaired t-test, $t_{(14)}$=-0.41, p=0.69, 95%CI=[-0.009,0.006], Cohen's d_s=0.20). As was the case for Group 5, we noted robust transfer of left arm aftereffects to the $N_{R,2}$ trials in Group 6 as well. Early $N_{R,2}$ trajectories were more curved (Fig. 5A, thick blue) and showed greater errors compared to early $N_{R,1}$ performance (paired t-test, $t_{(7)}$=12.32, p<0.0001, 95%CI=[13.138,19.382], Cohen's d_z=4.35, Table 2, Fig. 5I), but these errors became close to zero with subsequent null practice (Fig. 5B, thin blue). Most importantly, we noted that $CW_{R,2}$ learning was now substantially faster than

$CW_{R,1}$ learning (paired t-test, $t_{(7)}$=-4.57, 95%CI=[-0.083,-0.026], p=0.0026, Cohen's d_z=1.62, Table 1, Fig. 5J). This indicated that increasing the duration between $CW_{R,1}$ and $CCW_{L,1}$ training to 24 hours made the $CW_{R,1}$ memory resistant to interference from the competing $CCW_{L,1}$ memory and allowed faster recall the next day. Such a time-dependent pattern confirmed that interference between the memories developed by the two arms is indeed retrograde in nature.

DISCUSSION

The primary goal of this study was to investigate whether motor memories developed through learning with the two arms would interfere. We observed strong interference when the two arms adapted to opposing visuomotor rotations in close succession. We confirmed that this interference was retrograde in nature, since passage of time between the learning episodes with the two arms substantially reduced interference. These results further enhance our understanding of the neural organization of motor learning and also suggest that successive motor practice with two different limbs may prevent stabilization of newly acquired motor memories.

Few studies in the past have examined interference between competing motor memories developed through learning with different limbs. Moreover, these studies have often failed to reveal interference (Bock et al. 2005; Galea and Miall 2006). An important constraint in these studies however was that the arms were used in an alternating fashion on either every other trial or over a short set of trials. Thus, there was no opportunity for complete adaptation with one limb before learning with the other limb ensued, which may be essential for interference to be seen. In line with this thought, Stockinger et al. (2017) very recently demonstrated interference when the left arm was exposed to a force-field B following substantial adaptation of the right arm to an opposite force-field A. We also noted significant interference once subjects had undergone complete adaptation to the rotation, suggesting that substantial learning with the two arms may be essential to reveal interference.

While our results appear similar to those of Stockinger et al. (2017), important differences between the findings exist. Most crucial among these is Stockinger and colleagues' finding that the learning of B produced a deterioration of ~68% of the prior memory of A, while a control group that did not learn B showed a decrement of only about 15%. This difference was taken as evidence that B learning interfered with A. It may be argued however that while interference was present, it was not complete since ~32% of the memory of A was still intact, bringing into question the strength of the effect. In contrast, we observed complete interference; performance during the early trials of re-exposure to A ($CW_{R,2}$ for Group 1 and $CW_{L,2}$ for Group 3) was never biased towards prior A learning ($CW_{R,1}$ for Group 1 or $CW_{L,1}$ for Group 3), and was in fact biased away from the prior learning in Group 1. The reason for this difference between the studies could include previously described differences in force-field versus visuomotor adaptation (Krakauer et al. 1999; Rabe et al. 2009; Wang and Sainburg 2004b), differences in orientation of the visual display and availability of visual feedback of the limb, differences in when interference was assessed (24-hour gap in our study versus immediately after B learning in Stockinger et al. (2017)), and/or substantial but still incomplete adaptation to both A and B in their work. Nonetheless, both sets of results support the idea that interference can indeed occur when one arm adapts to a perturbation after the other arm has undergone substantial adaptation to an opposing perturbation. However, our current work goes further to newly reveal that interference occurs regardless of the order in which the arms learn, and that the interference is retrograde in nature; this represents a novel contribution of our study.

Mechanisms underlying retrograde effects

There are two potential reasons that might give rise to retrograde interference between motor memories developed with the two limbs. First, learning of rotation B may block the retrieval of the memory of rotation A learned earlier. In other words, the memory of A is intact, but motor memories may be subjected to recency effects where subjects simply retrieve the last memory developed in that learning context (i.e., the memory of B), leading to a suppression in the recall of A during re-exposure. It has been suggested that to prevent such effects and allow the expression of the (saved) memory, both A and B must be associated with distinct contextual cues during learning. Numerous studies have shown that such a contextual separation reduces interference, allowing the originally learned memory to be recalled successfully later (Cothros et al. 2009; Hirashima and Nozaki 2012; Howard et al. 2013; Nozaki et al. 2006; Sheahan et al. 2016). It has also been proposed that intrinsic cues that entail different sensorimotor transformations (for example, different body postures when learning A and B) work better than extrinsic ones (say different target colors for A and B). In line with this notion, Krakauer et al. (2006) have shown that learning two opposite rotations with different effectors within a limb (for example, wrist versus arm) produces no interference between the two competing memories developed in close succession. Associating the two perturbations with different limbs altogether should have therefore provided clearly distinct contextual cues, and allowed the memory of A to be expressed upon re-exposure if it was still present. However, this was not the case, and it therefore appears unlikely that the observed interference was because B learning blocked retrieval of an intact memory of A.

The second, and perhaps more likely explanation for retrograde effects in our case, is that the learning of B actually erased the prior memory of A because it required the same neural resources for adaptation. Past studies showing interference when A and B are learned with the *same* limb (Brashers-Krug et al. 1996; Krakauer et al. 2005; Overduin et al. 2006), have made a similar suggestion. Our current results lead us to submit that the same may be true even if adaptation occurs with *different* limbs. This idea is consistent with previous work that has demonstrated that a disruption in neural activity in a single brain region, for instance due to Stroke, produces deficits in visuomotor rotation learning regardless of the effector used to learn. In particular, parietal damage in the left, but not the right brain hemisphere, impairs visuomotor adaptation not just when the contralesional, right arm is used (Mutha et al. 2011b), but also when the ipsilesional, left arm is used to learn (Mutha et al. 2011a). Similar deficits have been found in patients with ideomotor apraxia, in whom maximum lesion overlap was in parietal cortex, and in fact, the extent of the learning deficit correlated with the volume of damage in inferior parietal regions (Mutha et al. 2017). These findings suggest a common neural substrate for learning with the two arms, and the interference observed in the current study is a pragmatic prediction of this kind of neural organization for visuomotor learning. Such a shared, lateralized substrate for the development of motor memories, as for other forms of memory (Tulving et al. 1994), may have evolved to optimize the use of existing neural resources. Interestingly, while this neural resource may be recruited for learning, the current findings also suggest that allowing time to pass, consolidates a newly formed memory and frees up this resource for new learning with another effector. It is plausible therefore that learning and longer-term retention of the memory may be dependent on different neural substrates, a thought echoed in the episodic memory literature as well (Eldridge et al. 2005; Gabrieli et al. 1997; Roy et al. 2017).

Obligatory, asymmetric interlimb transfer of learning

Although we did not explicitly set out to do so, we observed robust interlimb transfer of learning in the current study. This transfer was asymmetric and occurred only from the left to the right arm. In Groups 1 and 3, the right arm always showed larger errors initially when it followed left arm learning but not vice versa, while in Groups 5 and 6, only the early $N_{R,2}$ but not the early $N_{L,1}$ trials showed after effects in the direction of the previously trained arm movements; both sets of results provide evidence for asymmetric transfer. While addressing the mechanisms underlying the asymmetry, or even transfer itself, is not our goal here, a couple of relevant points must be mentioned. First, the asymmetry is broadly in line with prior work of Wang and Sainburg (2004b; 2003), who have consistently demonstrated transfer of visuomotor adaptation only from the left to the right arm in right-handers particularly when the two arms share workspaces, as was the case here. Second, unlike this past work, we noted that transfer was unavoidable, and was evident even on the first trial of right arm rotation exposure following left arm training. Wang and Sainburg (2004b) suggest that transfer on the first trial is not obligatory because the nervous system may use the first trial to probe whether prior learning would actually be useful in the new context and then decide whether to use that memory or not ("context" here refers to the condition where the right arm experiences either the same or opposite rotation following left arm adaptation): if prior learning is deemed helpful (for instance when the rotations are the same), transfer occurs, but if the learning is not useful (e.g., when the rotations are opposite), no transfer should occur. In the work of Wang and Sainburg, under conditions of opposite rotations, transfer was indeed negligible on the first trial, but it surprisingly did occur on subsequent trials to other targets, resulting in greater errors than naïve on those trials. In fact, in their work, errors of the right arm continued to remain greater for movements made to those targets for almost the entire learning block, but performance for the target used in the first trial was similar to naïve throughout. Thus, it appears that transfer did not occur *only* to the target used on the first trial, which is quite puzzling. This apparent lack of transfer could be due to movement direction dependent effects on initial direction errors (Gordon et al. 1994), and whether choice of a different target (or movement direction) on the first trial could have revealed the transfer more clearly remains an open question. Indeed, movement direction dependent modulation of transfer has recently been shown by Carroll et al. (2014). Thus, the systematic transfer seen on movements made to most targets in the work of Wang and Sainburg, combined with our current results, leads us to suggest that transfer from the left to the right arm is indeed obligatory.

Contributions of different learning mechanisms to interference

Prior work has emphasized that learning to adapt to perturbations such as visuomotor rotations used in the current study occurs via an error-driven update of an internal representation or model of the properties of the body, the environment and the interaction between the two (Gandolfo et al. 1996; Imamizu et al. 1995; Sainburg et al. 1999; Shadmehr and Mussa-Ivaldi 1994; Wang and Sainburg 2005). Newer studies have however argued that such adaptation may be driven by multiple processes that operate on top of the model-based learning mechanism, including explicit strategies and operant processes (Classen et al. 1998; Diedrichsen et al. 2010; Huang et al. 2011; Taylor et al. 2014). Even within a purely model-based learning framework, it has been posited that more than one error-sensitive process could be operational. In particular, “fast” and “slow” learning processes with different attributes, but both driven by error, have been proposed (Lee and Schweighofer 2009; Smith et al. 2006). Importantly, in most cases, these additional mechanisms have been invoked to explain savings, or faster re-learning of an arm when it is re-exposed to the same perturbing environment as original learning. At this stage, it is unclear – and we remain decidedly ambivalent – as to whether it is any of these mechanisms linked to savings that are shared, and give rise to transfer or interference effects across different effectors. We take this position primarily for two reasons. First, delineating exactly which mechanisms contribute to savings itself has been controversial given that it can be explained by model-based (Herzfeld et al. 2014; Smith et al. 2006) as well as non-model-based (Haith et al. 2015; Morehead et al. 2015) processes. Second, it is plausible that savings and transfer/interference are mediated by distinct neural processes (Leow et al. 2013). For instance, it has recently been postulated that transfer could be dependent on the slow learning process (Block and Celnik 2013), while savings could occur via a fast acting cognitive process linked to better action selection (Morehead et al. 2015). We therefore take a more parsimonious position and avoid extensive speculation about which particular learning mechanism might underlie the transfer/interference effects. We instead suggest that further dissection of the contributions of different learning mechanisms to these effects should be a topic of exciting future research.

CONCLUSIONS

To conclude, we provide clear evidence that learning opposing visuomotor rotations with different limbs leads to substantial interference between the newly developed motor memories. This interference is retrograde, and likely occurs because the two limbs compete for the same neural resources during learning.

This suggestion of a common neural basis for motor learning across different limbs is in line with our prior findings that have implicated inferior parietal regions of the left hemisphere as crucial for visuomotor learning regardless of the effector used to learn.

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FIGURE CAPTIONS

Fig. 1. *A,* Experimental setup comprising of a pseudo virtual reality system that restricted movements to the horizontal plane. Subjects performed arm reaching movements on a digitizing tablet while looking into a mirror placed between the tablet and a horizontally mounted HDTV. Feedback about hand position was displayed via the HDTV onto the mirror by means of a cursor. *B,* Trial structure across the different subject groups. Subjects in Group 1 (top-left panel) first adapted to a 30-degree clockwise rotation with their right arm ($CW_{R,1}$, red) followed by adaptation to a counterclockwise rotation with their left arm ($CCW_{L,1}$, green). They were then required to re-adapt to the clockwise rotation 24 hours later with their right arm ($CW_{R,2}$, blue). Subjects in Group 2 (top-right panel) first adapted to the same clockwise rotation with their right arm ($CW_{R,1}$, red) and were then directly re-exposed to the same rotation 24 hours later ($CW_{R,2}$, blue). This group thus did not use their left arm at all. Subjects in Group 3 (middle-left panel) adapted to the rotations in the reverse arm order. These subjects were first exposed to the clockwise rotation with their left arm ($CW_{L,1}$, red), and then adapted to a counterclockwise rotation with their right arm ($CCW_{R,1}$, green). They were then required to re-adapt to the original clockwise rotation, again with their left arm, 24 hours later ($CW_{L,2}$, blue). In contrast, subjects in Group 4 (middle-right panel) adapted to the clockwise rotation with their left arm ($CW_{L,1}$, red) and re-adapted to the same rotation 24 hours later with the same arm ($CW_{L,2}$, blue). This group thus did not undergo any adaptation with their right arm. In Experiment 2, subjects in Group 5 (bottom-left panel) first performed a set of null

trials with their right arm ($N_{R,1}$, red) and were then exposed to the clockwise rotation with the same arm ($CW_{R,1}$, red). After right arm adaptation, these subjects performed a set of null trials with their left arm ($N_{L,1}$, green), which was followed by adaptation to the counterclockwise rotation with the left arm ($CCW_{L,1}$, green). 24 hours later, these subjects were re-exposed to null trials with their right arm ($N_{R,2}$, blue) followed by re-exposure to the original clockwise rotation also with the right arm ($CW_{R,2}$, blue). Subjects in Group 6 (Experiment 3, bottom-right panel) followed the exact same paradigm as subjects in Group 5, except that the gap between the $N_{R,1}CW_{R,1}$ and the $N_{L,1}CCW_{L,1}$ trial sets was increased to 24 hours. All learning blocks comprised of 256 trials while all null blocks had 64 trials.

Fig. 2. Interference occurs when the two arms adapt to opposing rotations in close succession. *A:* Cursor trajectories on the first cycle of movements to the 8 targets during the $CW_{R,1}$ (thick red) and $CW_{R,2}$ (thick blue) blocks for subjects in Group 1. *B:* Cursor trajectories on the last cycle of the $CW_{R,1}$ (thin red) and $CW_{R,2}$ (thin blue) blocks. *C:* Cursor trajectories on the first cycle of movements of the $CCW_{L,1}$ (thick green) block and *D:* the last cycle of the $CCW_{L,1}$ block (thin green). Note that the order of the blocks was $CW_{R,1}$-$CCW_{L,1}$-$CW_{R,2}$, but the $CW_{R,1}$ and $CW_{R,2}$ trajectories are overlaid to clearly show the difference between them on the first cycle of movements. *E:* Change in mean direction error across trials for subjects in Group 1. Error bars represent SEM across subjects. The red, green and blue profiles represent the $CW_{R,1}$, $CCW_{L,1}$ and the $CW_{R,2}$ learning blocks

respectively. Inset shows errors across cycles (mean of 8 movements) for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors in $CW_{R,2}$ were greater initially compared to $CW_{R,1}$ errors. *F:* Mean ±SEM learning rate for the $CW_{R,1}$ (red), $CCW_{L,1}$ (green) and $CW_{R,2}$ (blue) blocks for Group 1. Dots represent the learning rate for individual subjects. *G:* Cursor trajectories on the first cycle of movements for subjects in Group 2 during the $CW_{R,1}$ (red) and $CW_{R,2}$ (blue) learning blocks. These subjects did not undergo any adaptation with their left arm between these two right arm adaptation blocks. H: Cursor trajectories on the last cycle for these subjects. I: Change in mean direction error across trials for subjects in Group 2. Error bars represent SEM across subjects. The red and blue profiles represent the $CW_{R,1}$ and $CW_{R,2}$ blocks respectively. Inset shows errors across cycles for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors in $CW_{R,2}$ were smaller initially compared to $CW_{R,1}$ errors in these subjects.

Fig. 3. Interference also occurs when the two arms are used in the reverse order *A:* Cursor trajectories on the first cycle of movements to the 8 targets during the $CW_{L,1}$ (thick red) and $CW_{L,2}$ (thick blue) blocks for subjects in Group 3. *B:* Cursor trajectories on the last cycle of the $CW_{L,1}$ (thin red) and $CW_{L,2}$ (thin blue) blocks. *C:* Cursor trajectories on the first cycle of movements of the $CCW_{R,1}$ (thick green) block and *D:* the last cycle of the $CCW_{R,1}$ block (thin green). Note that the order of the blocks was $CW_{L,1}$-$CCW_{R,1}$-$CW_{L,2}$, but the $CW_{L,1}$ and $CW_{L,2}$ trajectories are overlaid to clearly show the overlap between them on the first cycle of

movements. *E:* Change in mean direction error across trials for subjects in Group 3. Error bars represent SEM across subjects. The red, green and blue profiles represent the $CW_{L,1}$, $CCW_{R,1}$ and the $CW_{L,2}$ learning blocks respectively. Inset shows errors across cycles for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors in CWL,2 were similar to CWL,1 errors. *F:* Mean±SEM learning rate for the $CW_{L,1}$ (red), $CCW_{R,1}$ (green) and $CW_{L,2}$ (blue) blocks for Group 1. Dots represent the learning rate for individual subjects. *G:* Cursor trajectories on the first cycle of movements to the 8 targets for subjects in Group 4 during the $CW_{L,1}$ (red) and $CW_{L,2}$ (blue) learning blocks. These subjects did not undergo any adaptation with their right arm between these two left arm adaptation blocks. H: Cursor trajectories on the last cycle for these subjects. I: Change in mean direction error across trials for subjects in Group 4. Error bars represent SEM across subjects. The red and blue profiles represent the $CW_{L,1}$ and $CW_{L,2}$ learning blocks respectively. Inset shows errors across cycles for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors in $CW_{L,2}$ were smaller initially compared to CWL,1 errors in these subjects.

Fig. 4. Transfer of left arm learning to the right arm and persistence of interference despite washout in Group 5. *A:* Cursor trajectories on the first cycle of movements to the 8 targets during the $N_{R,1}$ (thick red) and $N_{R,2}$ (thick blue) blocks for subjects in Group 5. *B:* Cursor trajectories on the last cycle of the $N_{R,1}$ (thin red) and $N_{R,2}$ (thin blue) blocks. *C:* Cursor trajectories on the first cycle of movements to the 8 targets during the $CW_{R,1}$ (thick red) and $CW_{R,2}$ (thick blue)

learning blocks. *D:* Cursor trajectories on the last cycle of movements of the $CW_{R,1}$ (thin red) and $CW_{R,2}$ (thin blue) blocks. *E:* Cursor trajectories on the first cycle of movements during the $N_{L,1}$ (thick green) block and *F:* the last cycle of the $N_{L,1}$ (thin green) blocks. *G:* Cursor trajectories on the first cycle of movements of the $CCW_{L,1}$ (thick green) block and *H:* the last cycle of the $CCW_{L,1}$ block (thin green). Note that the task was performed in the $N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CCW_{R,2}$ order, but trajectories of the $N_{R,1}$ and $N_{R,2}$ blocks as well as the $CW_{R,1}$ and $CW_{R,2}$ blocks have been overlaid so that they can be compared easily. *I:* Change in mean direction error across trials for subjects in Group 5. Error bars represent SEM across subjects. The $N_{R,1}$ and $CW_{R,1}$ trials are shown in red, the $N_{L,1}$ and $CCW_{L,1}$ trials are shown in green and the $N_{R,2}$ and $CW_{R,2}$ trials are shown in blue. Inset shows errors across cycles for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors are larger in $N_{R,2}$ compared to $N_{R,1}$, and that the $CW_{R,1}$ and $CW_{R,2}$ learning curves overlap. J*:* Mean±SEM learning rate for $CW_{R,1}$ (red), $CCW_{L,1}$ (green) and $CW_{R,2}$ (blue) learning. Dots represent the learning rate for individual subjects. There was no statistically significant difference between the learning rates.

Fig. 5. Reduced interference in Group 6 when 24 hours separate $CW_{R,1}$ and $CCW_{L,1}$ learning. *A:* Cursor trajectories on the first cycle of movements to the 8 targets during the $N_{R,1}$ (thick red) and $N_{R,2}$ (thick blue) blocks for subjects in Group 6. *B:* Cursor trajectories on the last cycle of the $N_{R,1}$ (thin red) and $N_{R,2}$ (thin blue) blocks. *C:* Cursor trajectories on the first cycle of movements to the 8

targets during the $CW_{R,1}$ (thick red) and $CW_{R,2}$ (thick blue) learning blocks. *D:* Cursor trajectories on the last cycle of movements of the $CW_{R,1}$ (thin red) and $CW_{R,2}$ (thin blue) blocks. *E:* Cursor trajectories on the first cycle of movements during the $N_{L,1}$ (thick green) block and *F:* the last cycle of the $N_{L,1}$ (thin green) blocks. *G:* Cursor trajectories on the first cycle of movements of the $CCW_{L,1}$ (thick green) block and *H:* the last cycle of the $CCW_{L,1}$ block (thin green). Note that the task was performed in the $N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CCW_{R,2}$ order, but trajectories of the $N_{R,1}$ and $N_{R,2}$ blocks, as well as the $CW_{R,1}$ and $CW_{R,2}$ blocks have been overlaid so that they can be compared easily. *I:* Change in mean direction error across trials for subjects in Group 6. Error bars represent SEM across subjects. The $N_{R,1}$ and $CW_{R,1}$ trials are shown in red, the $N_{L,1}$ and $CCW_{L,1}$ trials are shown in green and the $N_{R,2}$ and $CW_{R,2}$ trials are shown in blue. Inset shows errors across cycles for the first 15 cycles. Shaded area in the inset represents SEM. Note that the errors are larger in $N_{R,2}$ compared to $N_{R,1}$ and that $CW_{R,2}$ learning is faster than $CW_{R,1}$ learning. J*:* Mean±SEM learning rate for $CW_{R,1}$ (red), $CCW_{L,1}$ (green) and $CW_{R,2}$ (blue) learning. Dots represent the learning rate for individual subjects. Statistical analysis confirmed faster learning during $CW_{R,2}$.

Figure 1

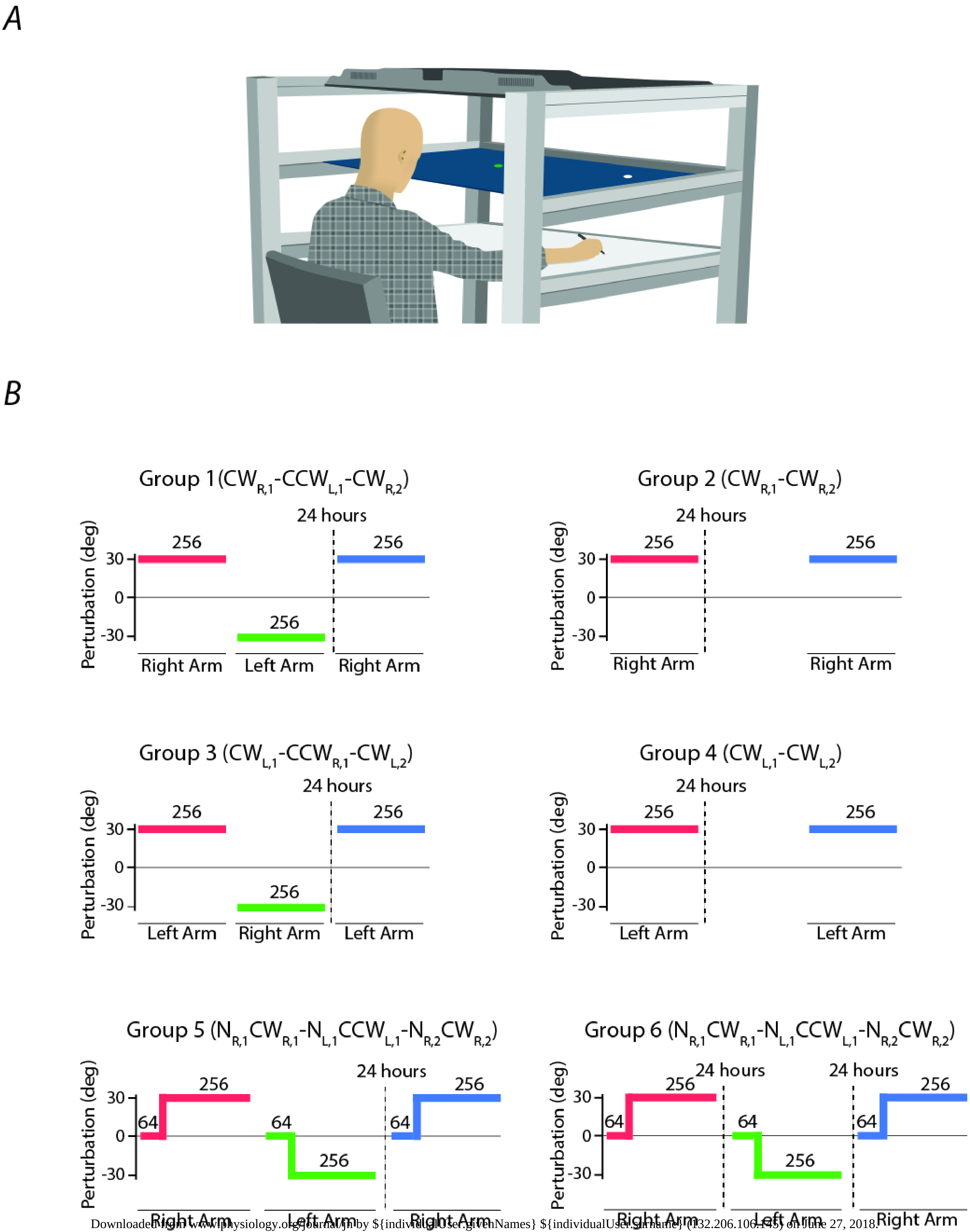
A
B
Group 1 ($CW_{R,1}$-$CCW_{L,1}$-$CW_{R,2}$)
24 hours
256
256
256
30
0
-30
Perturbation (deg)
Right Arm
Left Arm
Right Arm
Group 2 ($CW_{R,1}$-$CW_{R,2}$)
24 hours
256
256
30
0
-30
Perturbation (deg)
Right Arm
Right Arm
Group 3 ($CW_{L,1}$-$CCW_{R,1}$-$CW_{L,2}$)
24 hours
256
256
256
30
0
-30
Perturbation (deg)
Left Arm
Right Arm
Left Arm
Group 4 ($CW_{L,1}$-$CW_{L,2}$)
24 hours
256
256
30
0
-30
Perturbation (deg)
Left Arm
Left Arm
Group 5 ($N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CW_{R,2}$)
24 hours
64
256
64
256
64
256
30
0
-30
Perturbation (deg)
Right Arm
Left Arm
Right Arm
Group 6 ($N_{R,1}CW_{R,1}$-$N_{L,1}CCW_{L,1}$-$N_{R,2}CW_{R,2}$)
24 hours
24 hours
64
256
64
256
64
256
30
0
-30
Perturbation (deg)
Right Arm
Left Arm
Right Arm

Figure 2

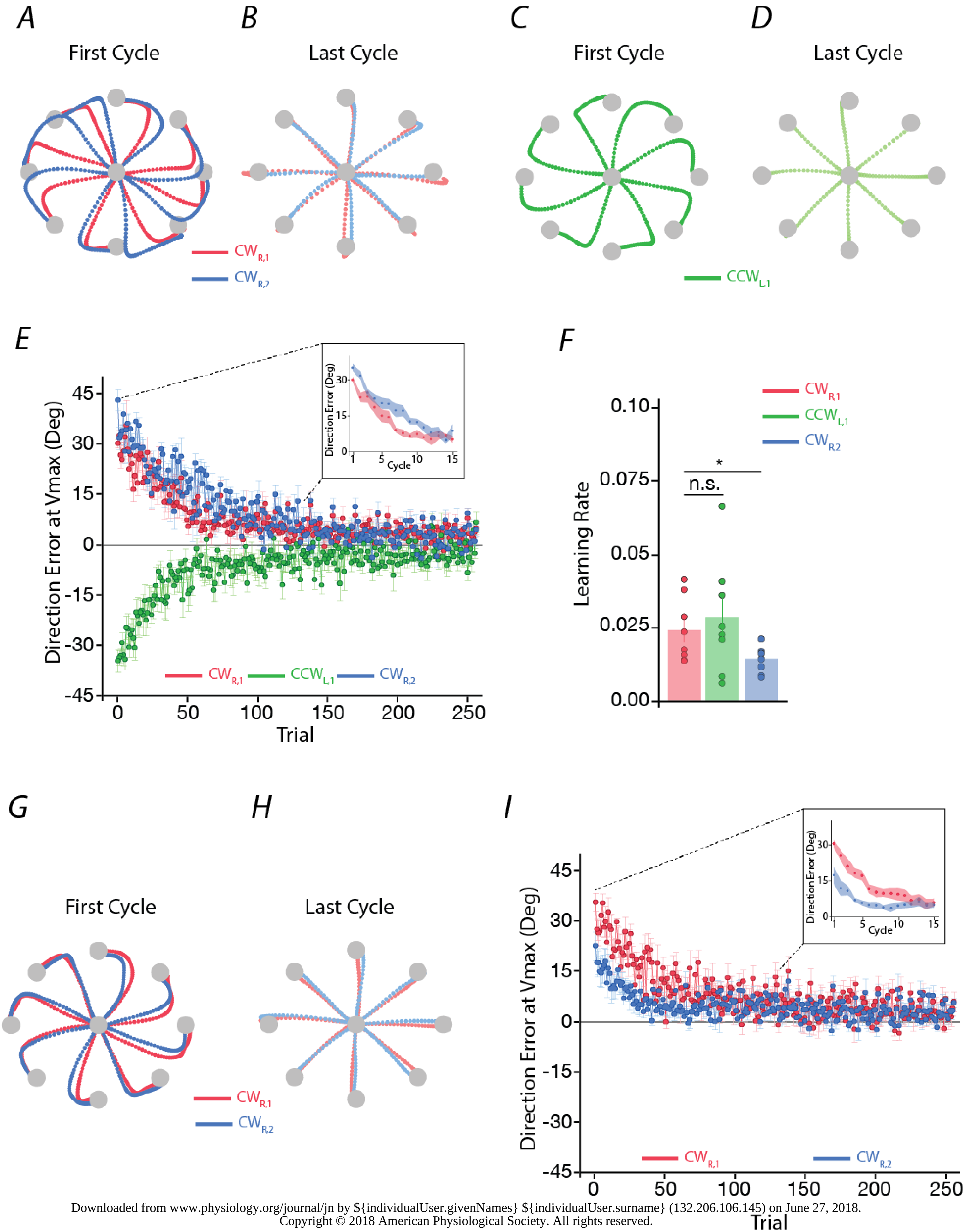
A
First Cycle
B
Last Cycle
CW$_{R,1}$
CW$_{R,2}$
C
First Cycle
D
Last Cycle
CCW$_{L,1}$
E
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
Trial
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
CW$_{R,1}$
CCW$_{L,1}$
CW$_{R,2}$
F
Learning Rate
0.10
0.075
0.05
0.025
0.00
*
n.s.
CW$_{R,1}$
CCW$_{L,1}$
CW$_{R,2}$
G
First Cycle
H
Last Cycle
CW$_{R,1}$
CW$_{R,2}$
I
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
Trial
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
CW$_{R,1}$
CW$_{R,2}$

Figure 3

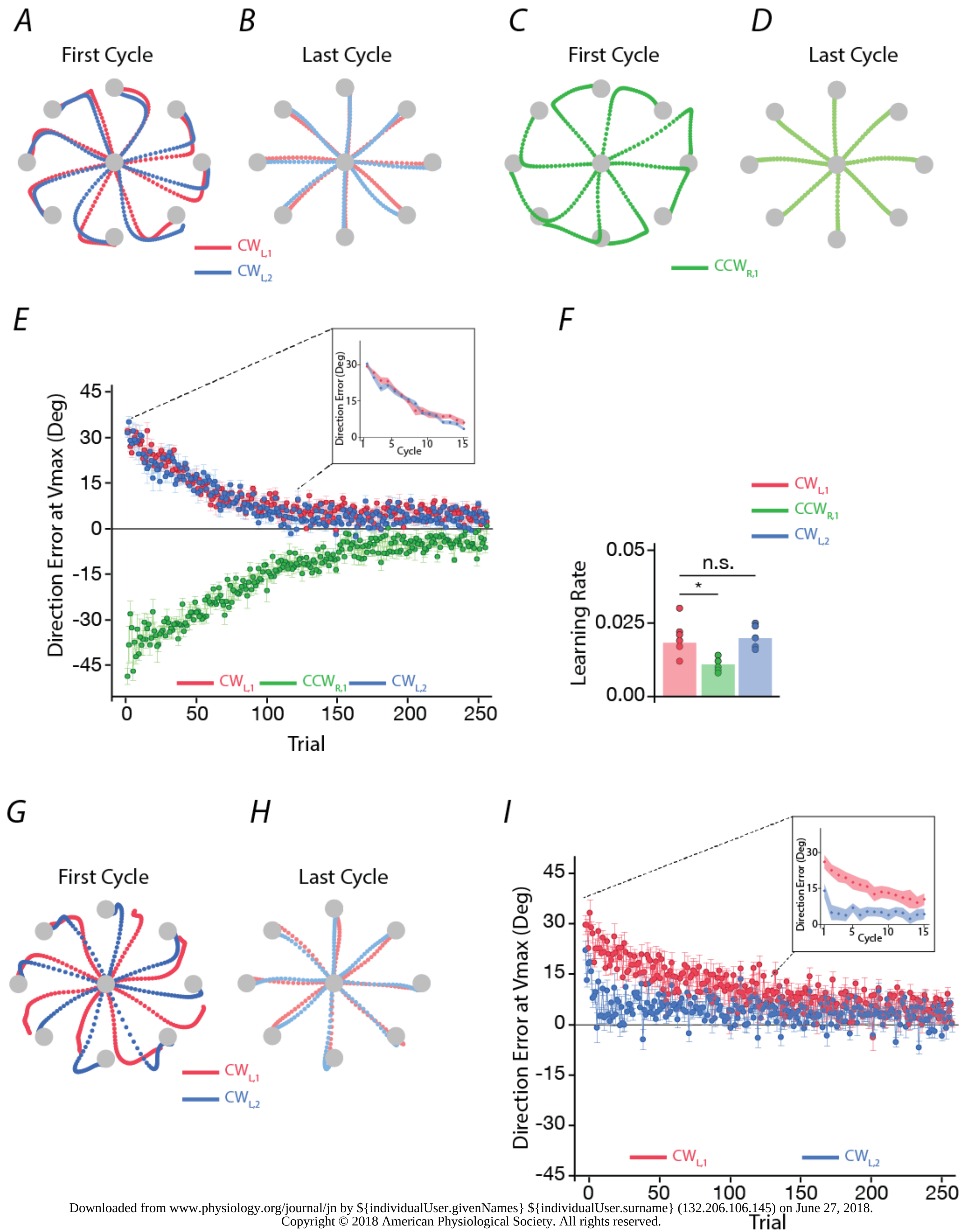
A
First Cycle
CW$_{L,1}$
CW$_{L,2}$
B
Last Cycle
C
First Cycle
CCW$_{R,1}$
D
Last Cycle
E
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
Trial
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
CW$_{L,1}$
CCW$_{R,1}$
CW$_{L,2}$
F
CW$_{L,1}$
CCW$_{R,1}$
CW$_{L,2}$
Learning Rate
0.05
0.025
0.00
n.s.
*
G
First Cycle
CW$_{L,1}$
CW$_{L,2}$
H
Last Cycle
I
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
Trial
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
CW$_{L,1}$
CW$_{L,2}$

Figure 4

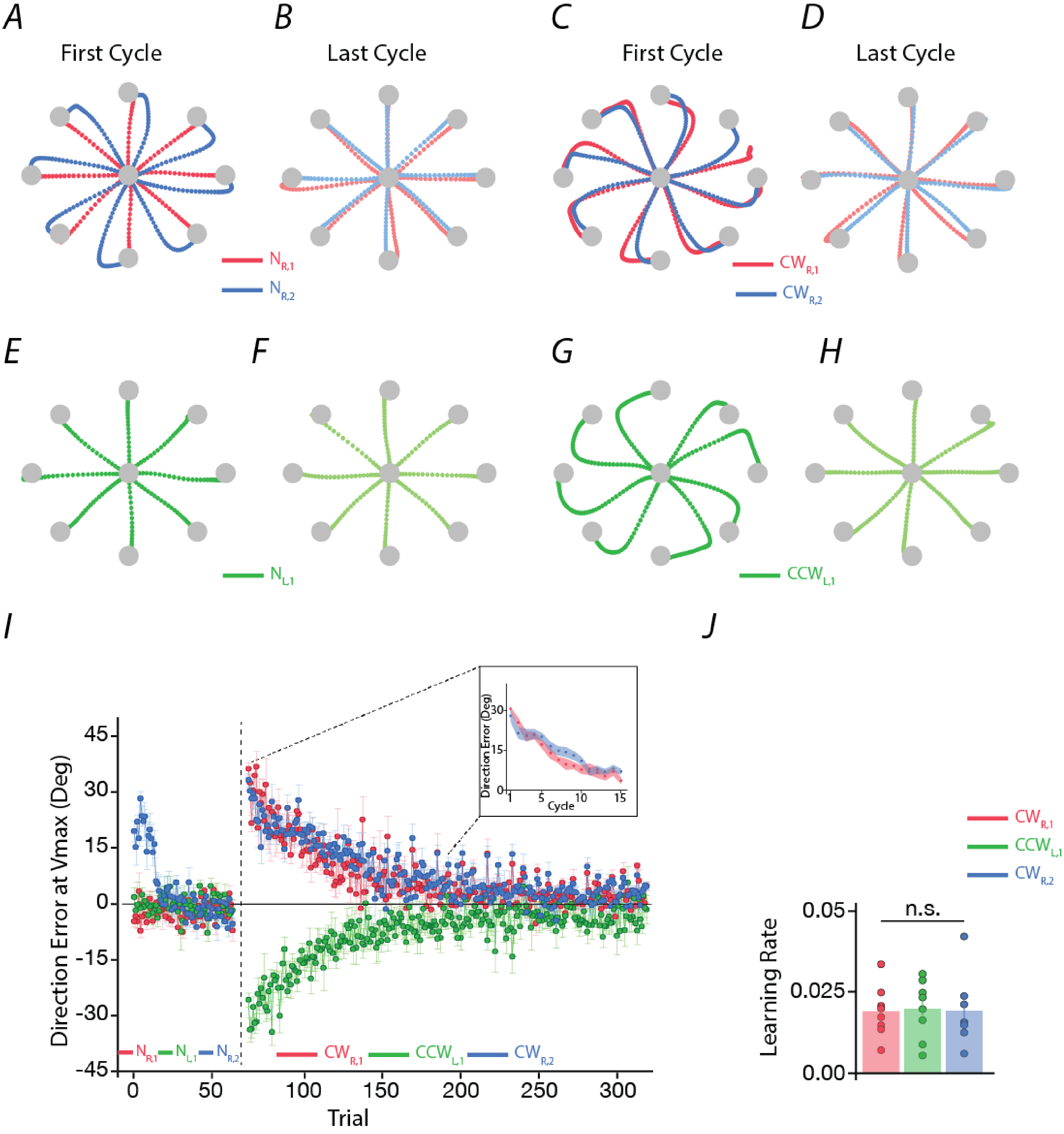
A
First Cycle
B
Last Cycle
C
First Cycle
D
Last Cycle
$N_{R,1}$
$N_{R,2}$
$CW_{R,1}$
$CW_{R,2}$
E
F
G
H
$N_{L,1}$
$CCW_{L,1}$
I
J
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
300
Trial
$N_{R,1}$
$N_{L,1}$
$N_{R,2}$
$CW_{R,1}$
$CCW_{L,1}$
$CW_{R,2}$
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
$CW_{R,1}$
$CCW_{L,1}$
$CW_{R,2}$
Learning Rate
0.05
0.025
0.00
n.s.

Figure 5

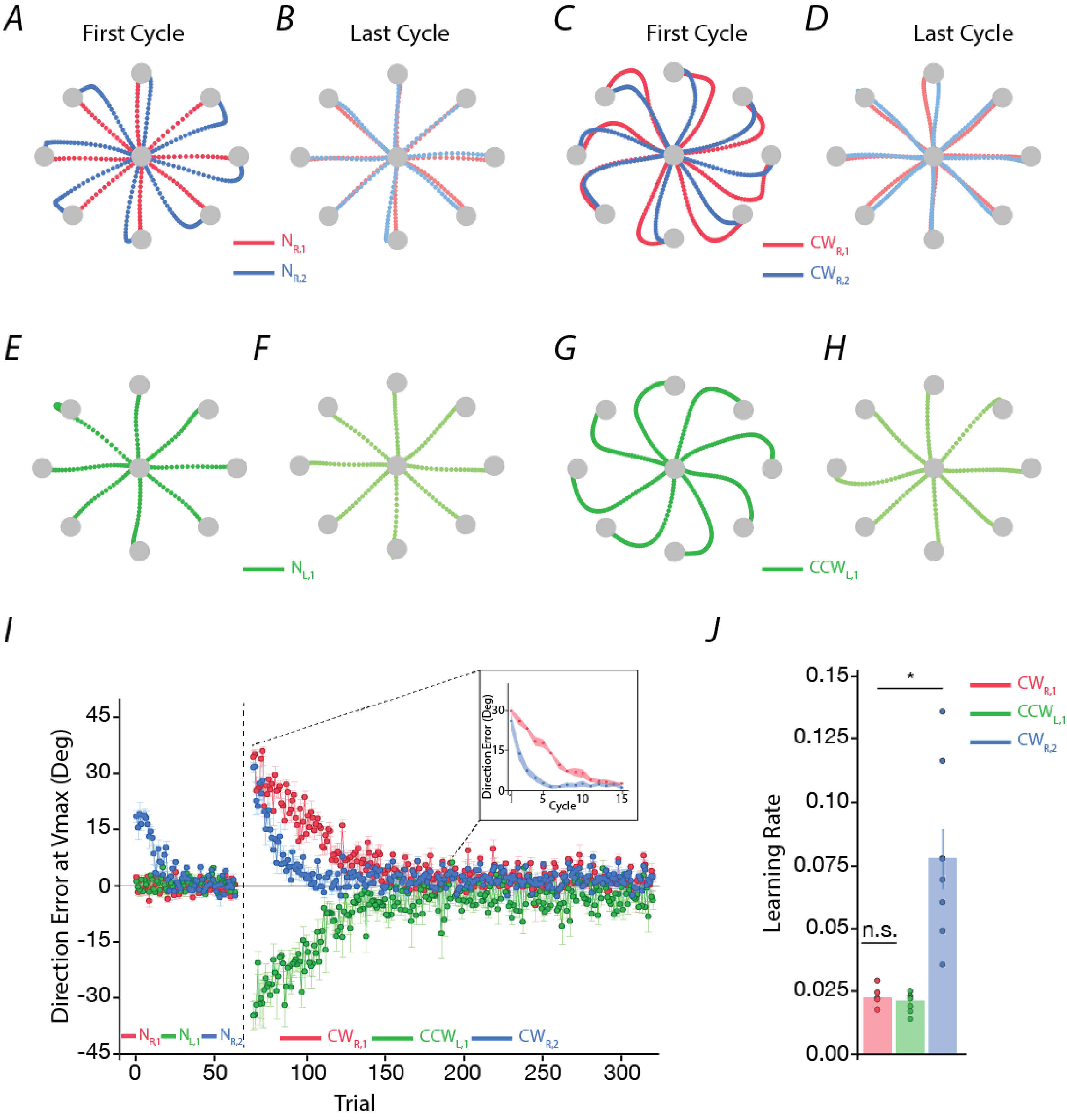
A
First Cycle
B
Last Cycle
C
First Cycle
D
Last Cycle
$N_{R,1}$
$N_{R,2}$
$CW_{R,1}$
$CW_{R,2}$
E
F
G
H
$N_{L,1}$
$CCW_{L,1}$
I
Direction Error at Vmax (Deg)
45
30
15
0
-15
-30
-45
0
50
100
150
200
250
300
Trial
N_{R1}
N_{L1}
$N_{R,2}$
$CW_{R,1}$
CCW_{L1}
$CW_{R,2}$
Direction Error (Deg)
30
15
0
1
5
10
15
Cycle
J
Learning Rate
0.15
0.125
0.10
0.075
0.05
0.025
0.00
n.s.
*
$CW_{R,1}$
$CCW_{L,1}$
$CW_{R,2}$

Table 1

Experiment	Group	Learning Block	Movement Duration (msec)	Learning Rate	R^2 of fit
Experiment 1	Group 1	$CW_{R,1}$	905±106	0.024±0.004	0.89±0.06
		$CCW_{L,1}$	960±103	0.028±0.007	0.80±0.08
		$CW_{R,2}$	948±111	0.014±0.002	0.86±0.07
	Group 3	$CW_{L,1}$	665±111	0.018±0.002	0.73±0.05
		$CCW_{R,1}$	787±13	0.011±0.001	0.87±0.06
		$CW_{L,2}$	863±47	0.019±0.001	0.76±0.07
Experiment 2	Group 5	$CW_{R,1}$	915±103	0.018±0.002	0.81±0.07
		$CCW_{L,1}$	975±113	0.02±0.003	0.89±0.07
		$CW_{R,2}$	923±108	0.019±0.004	0.87±0.08
Experiment 3	Group 6	$CW_{R,1}$	761±11	0.022±0.002	0.84±0.06
		$CCW_{L,1}$	716±19	0.021±0.001	0.86±0.06
		$CW_{R,2}$	648±5	0.078±0.012	0.78±0.09

Table 2

Experiment	Group	Learning Block	Direction Error on First Trial
Experiment 1	Group 1	$CW_{R,1}$	31.17±1.17
		$CCW_{L,1}$	-34.69±3.26
		$CW_{R,2}$	43.12±3.12
	Group 2	$CW_{R,1}$	35.52±2.79
		$CW_{R,2}$	22.50±4.20
	Group 3	$CW_{L,1}$	32.04±0.72
		$CCW_{R,1}$	-48.68±2.64
		$CW_{L,2}$	31.43±1.58
	Group 4	$CW_{L,1}$	29.47±2.81
		$CW_{L,2}$	21.32±2.51
Experiment 2	Group 5	$N_{R,1}$	-4.72±1.35
		$CW_{R,1}$	36.21±1.57
		$N_{L,1}$	1.76±2.53
		$CCW_{L,1}$	-25.85±1.91
		$N_{R,2}$	19.49±2.81
		$CW_{R,2}$	33.17±1.86
Experiment 3	Group 6	$N_{R,1}$	1.98±0.78
		$CW_{R,1}$	34.35±1.76
		$N_{L,1}$	0.89±1.57
		$CCW_{L,1}$	-34.78±3.74
		$N_{R,2}$	18.24±1.66
		$CW_{R,2}$	31.61±1.29