Savings Upon Re-Aiming in Visuomotor Adaptation

J. Ryan Morehead, Matthew J. Crossley, Richard B. Ivry

Standard models of sensorimotor adaptation make the fundamental assumption that this learning is error-based (EB) and incremental. However, a growing literature points to the operation of multiple learning processes in adaptation tasks (Wolpert, Diedrichsen & Flanagan, 2011). For example, savings upon relearning of a visuomotor rotation -- even after an extended return to baseline conditions -- is commonly observed in humans, yet cannot be accounted for with simple EB models. We hypothesize that savings in such tasks reflects a re-aiming process that is fundamentally distinct from EB adaptation. Specifically, it is flexible, under volitional control, and supports broad generalization. We present four experiments that support this hypothesis.

Experiment 1 examined within-session savings as subjects reached to two targets at four different visuomotor rotation magnitudes: 15, 30, 45 and 60 degrees (Fig. 1A, B). Savings was only observed in the 45 and 60 deg groups (Fig. 1C, $p < .001$). We hypothesize that the large errors initially experienced in these groups were sufficiently salient to induce the exploration of aiming strategies to compensate for the rotation (e.g., aim somewhere other than the target). While this exploratory process was variable during the first exposure to the rotation, savings arises because a successful strategy can be quickly recalled during the second exposure to the rotation.

In Exp. 2, we examined the effect of asking participants to volitionally stop re-aiming. Two epochs with a 45° rotation were separated by 100 washout trials (Fig. 2A). Before the seventh trial of the second rotation epoch, the experimenter interrupted the task, giving the following verbal instructions: "The perturbation to your cursor that was just turned on will now be off for the next two trials. I want you to aim directly for the target and reach directly for the target for the next two movements." Subsequent to these two movements, the subjects were told "The perturbation is back on" and were allowed to continue reaching for the duration of the task. There was a marked difference of the mean hand position between the intervention trials and the two trials immediately preceding the verbal intervention (Fig. 2C, $p < .0005$), consistent with the hypothesis that the observed savings is based on a re-aiming that is under volitional control.

In Exp. 3, we asked if participants could flexibly switch between aiming strategies based on arbitrary cues. Previous work has shown that pure EB adaptation is insensitive to such cues without extensive training (Cunningham & Welch, 1994). Two rotation blocks were separated by 100 washout trials (Fig. 3A). There were two types of trials in the rotation blocks, indicated by the cursor color. When the cursor was red (70 trials), the rotation was present; when white (10 trials), the rotation was absent. The participants were instructed at the start of the experiment, "Later on your cursor will occasionally turn red, which means that something weird will happen on that trial. On those trials you will still try to do the same thing as a normal trial, which is hit the target with your cursor." Our focus was on how performance changed on the rotation-free probe trials as compared to the immediately-preceding rotation trials. For the 45° group there was a large reliable difference between the two trial types (Fig.3C, $p <.005$), indicating that subjects were readily able to use the contextual cue to switch between the two conditions. Moreover, savings in the second rotation block was restricted to the rotation trials ($p <.005$). The 15° group did not show a significant difference between the two trial types ($p = .241$), and did not display evidence of savings for either trial type.

Exp. 4 looked at generalization, asking how participants responded when presented in a second rotation block with a perturbation in the opposite direction of that used in the first rotation block. Two groups of participants were initially trained with either a 45° or 15° counter-clockwise rotation, followed by 160 washout trials. Participants in both groups were then tested with a 30° clockwise rotation (Fig. 4A). Surprisingly, the 45° group responded to the second rotation by moving towards the previous aiming/handspace solution (Fig. 4C, $p < .05$), consistent with recall of a memory for a previous aiming plan. Following this initial response, the 45° group rapidly adjusted their performance and showed faster learning (savings) than the group exposed to a 15° rotation (Fig. 4B, $p < .05$). Notably the ideal final hand position for this new rotation had not been experienced; as such, earlier reinforcement of a specific hand space solution cannot explain the savings observed in this experiment.

In summary, the results demonstrate a novel mechanism for savings in sensorimotor adaptation tasks, namely that savings can arise from the selection of a previously used aiming plan. Participants were able to flexibly invoke an aiming process, changing the desired action based on context. This process can operate independently of recent error history. Most striking, this process supported generalization to a new environment when a previously used strategy was inappropriate for a novel perturbation. The contribution of action selection (such as an aiming strategy) in sensorimotor adaptation tasks has been under-appreciated. Consideration of such processes can help predict why and when behavioral results will diverge from predictions derived from EB models of visuomotor adaptation.

References:

Wolpert, Diedrichsen & Flanagan (2011) *Nat Rev Neurosci* 12:739-751.
Cunningham & Welch (1994) *Hum Percept Perform*, *20*(5), 987.

Experiment 1. Savings for Large, Not Small, Rotations

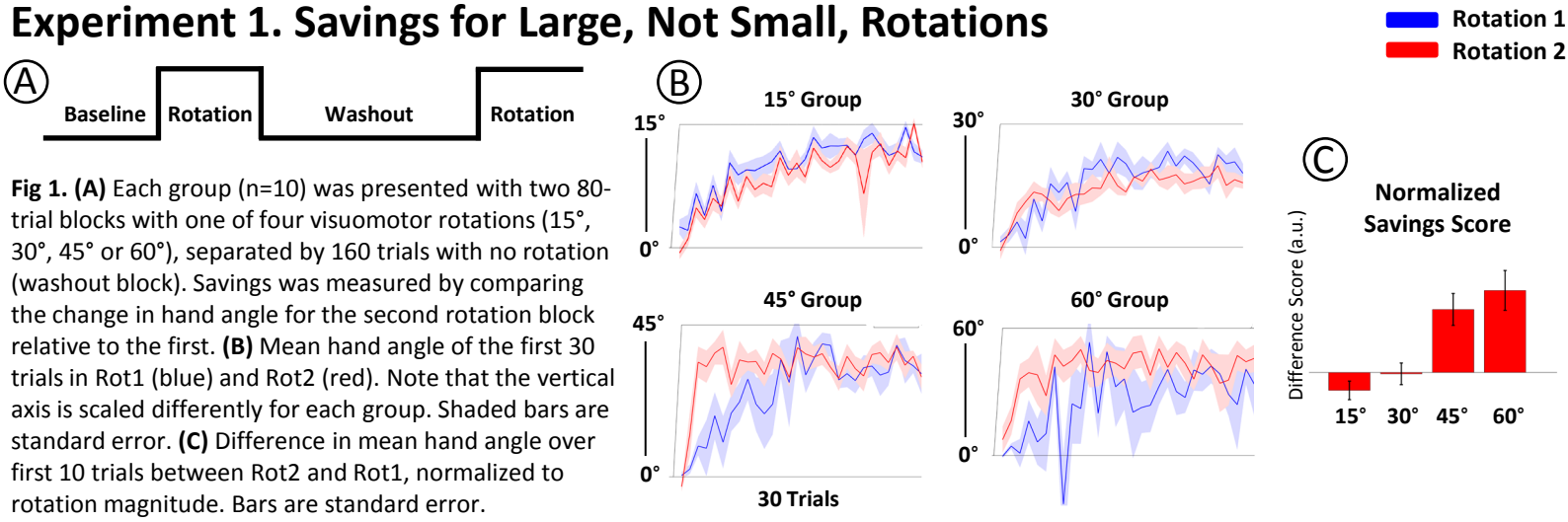

Fig 1. (A) Each group (n=10) was presented with two 80-trial blocks with one of four visuomotor rotations (15°, 30°, 45° or 60°), separated by 160 trials with no rotation (washout block). Savings was measured by comparing the change in hand angle for the second rotation block relative to the first. **(B)** Mean hand angle of the first 30 trials in Rot1 (blue) and Rot2 (red). Note that the vertical axis is scaled differently for each group. Shaded bars are standard error. **(C)** Difference in mean hand angle over first 10 trials between Rot2 and Rot1, normalized to rotation magnitude. Bars are standard error.

Experiment 2. Stop Aiming Task

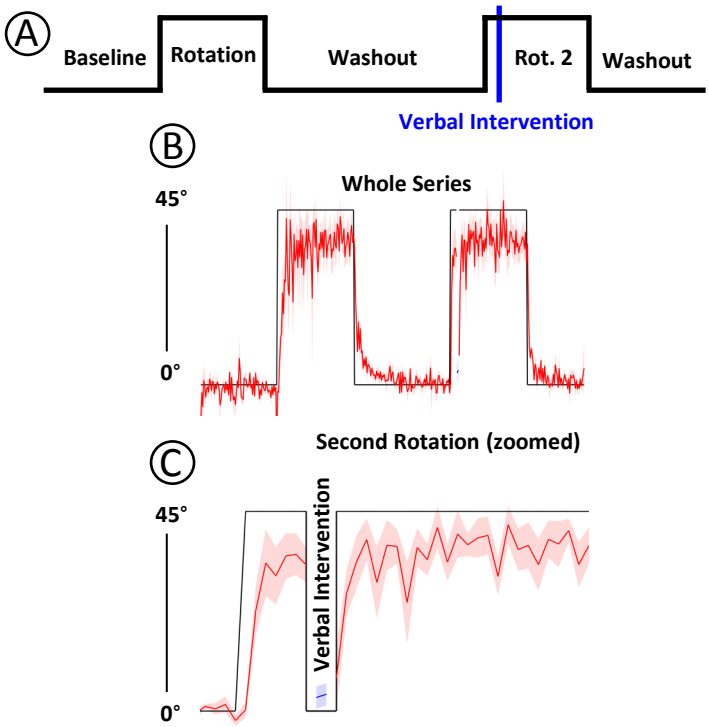

Fig. 2 (A) At the seventh trial of Rotation 2, participants (n=10) were told to move directly to the target. **(B)** Mean hand angle for the entire experiment. **(C)** Mean hand angle for Rotation 2, including the two intervention trials.

Experiment 3. Color Cueing Task

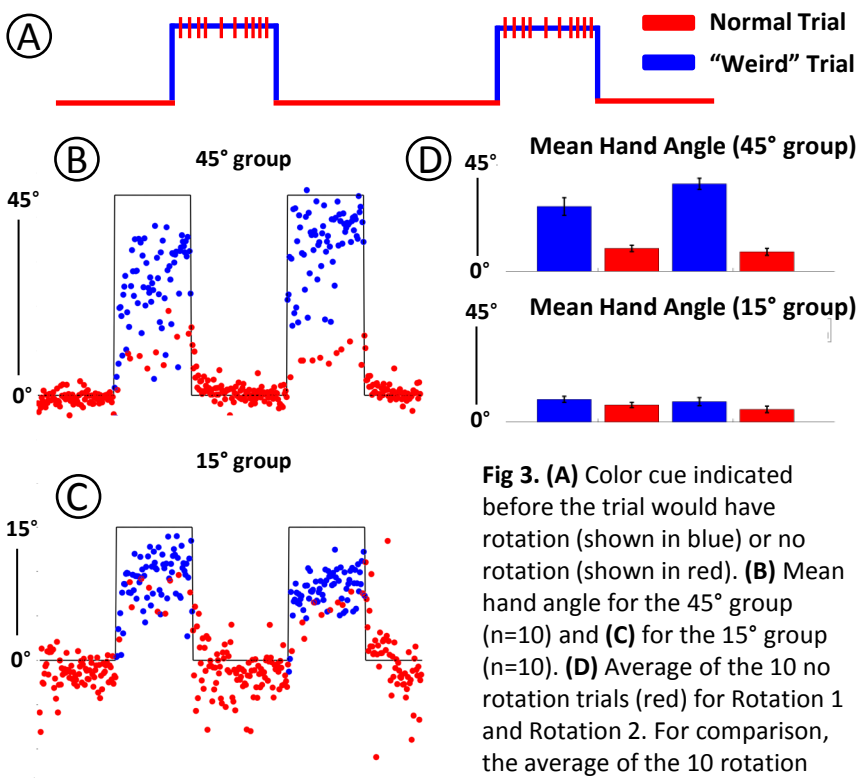

Fig 3. (A) Color cue indicated before the trial would have rotation (shown in blue) or no rotation (shown in red). **(B)** Mean hand angle for the 45° group (n=10) and **(C)** for the 15° group (n=10). **(D)** Average of the 10 no rotation trials (red) for Rotation 1 and Rotation 2. For comparison, the average of the 10 rotation trials preceding each no rotation trial is shown (blue).

Experiment 4. Savings for an Opposite Rotation

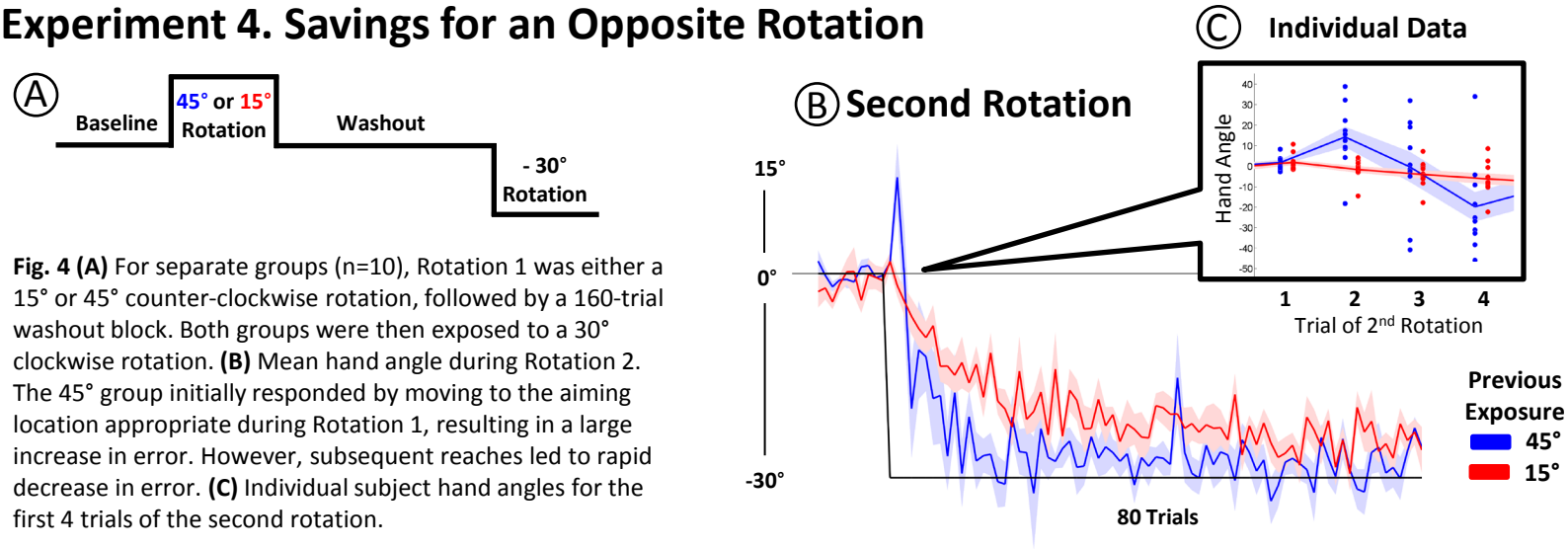

Fig. 4 (A) For separate groups (n=10), Rotation 1 was either a 15° or 45° counter-clockwise rotation, followed by a 160-trial washout block. Both groups were then exposed to a 30° clockwise rotation. **(B)** Mean hand angle during Rotation 2. The 45° group initially responded by moving to the aiming location appropriate during Rotation 1, resulting in a large increase in error. However, subsequent reaches led to rapid decrease in error. **(C)** Individual subject hand angles for the first 4 trials of the second rotation.