

## Mental Rotation as a Behavioral and Neural Model of Explicit Aiming During Visuomotor Learning

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Recent research has highlighted the role of explicit aiming processes in visuomotor rotation (VMR) tasks, showing that the learning curve arises from a combination of explicit aiming and implicit adaptation (see McDougle et al., 2016 for a review). While a great deal of attention has focused on characterizing the latter process — developing elegant models for the implicit adaptation of a forward model — less attention has focused on characterizing the aiming process. How do people explicitly re-aim their intended movement, away from the cued visual target, in order to rapidly counter a visuomotor rotation?

The seminal findings of Shepard & Metzler (1971) revealed that when subjects are asked to determine the identity of a rotated object, their reaction time (RT) increases linearly with the magnitude of the object's rotation. This finding suggested that an “analog” computation is being performed; that is, a mental representation of the object was itself, in a sense, being rotated. While at face value this result seems unrelated to studies of sensorimotor adaptation, Pellizzer & Georgopoulos (1991) showed that when human subjects are explicitly instructed to perform reaching movements directed at different angles relative to a visual target, an increase in the instructed angle led to a linear increase in RT. The findings from this motor variant of a mental rotation task showed remarkable similarity to a classic mental rotation task, involving alphabetical letters, suggesting that similar computational processes were involved. Furthermore, using a similar reaching task in a monkey, Georgopoulos et al. (1989) showed that a directionally-tuned population vector in M1 traverses intermediate angles during preparation of a rotated reach.

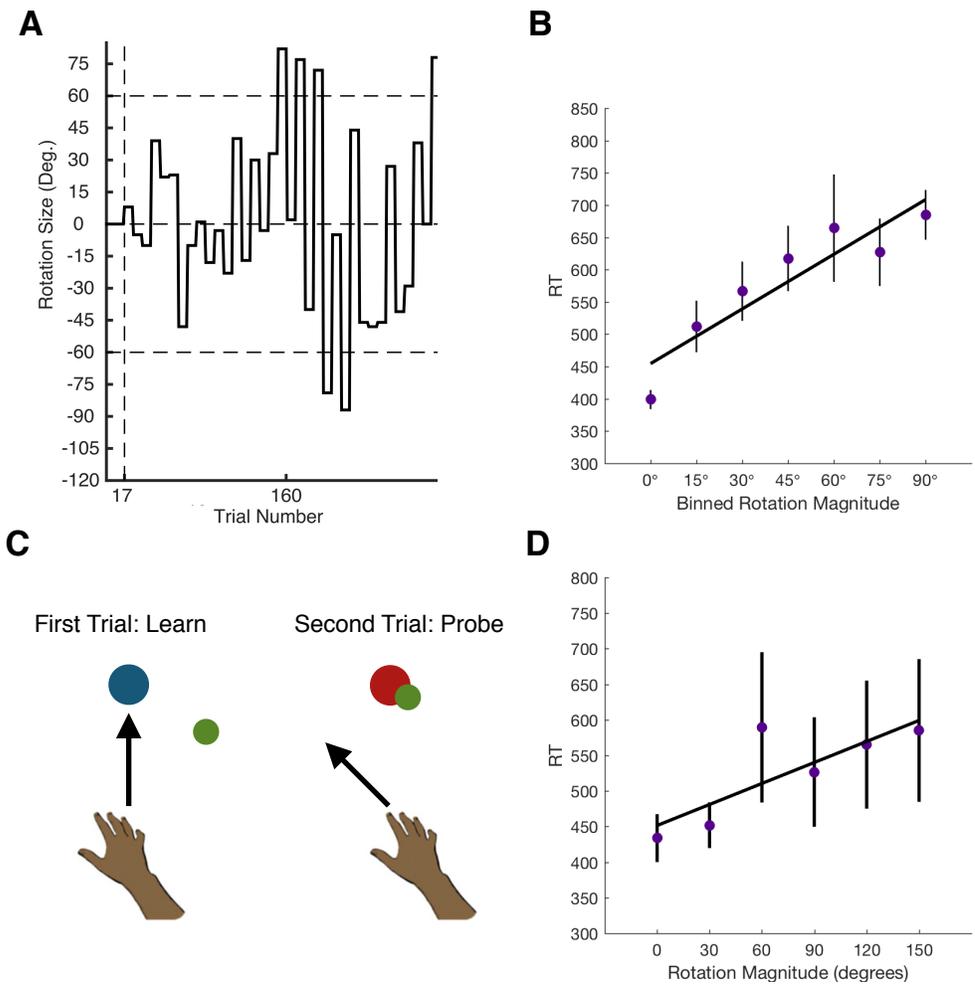
If a form of mental rotation underlies the aiming process in VMR, it follows that the magnitude of an imposed rotation perturbation in a VMR task should predict RT. We analyzed subjects' reaction times from a previous structural learning experiment (Bond & Taylor, SFN 2015), which involved pseudorandomly presenting rotations of varying magnitudes in brief cycles (Fig. 1A). We binned the absolute values of each random rotation magnitude by increments of 15° and plotted it against RT, which is defined in all following analyses as the time it takes subjects to initiate their movement after target appearance. As shown in Fig. 1B, we found a strong positive linear relationship between rotation magnitude and RT ( $\mu$  regression coefficient = 3.57,  $p < 0.001$ ).

To further test this relationship, we recruited nine participants to perform a motor-variant of a mental rotation task in which participants reached to visual targets while sliding their right hand across a digitizing tablet. In this task, subjects performed 144 trial “pairs”. On the first trial of a pair, a target appeared and subjects were instructed to reach directly to the target to observe where the resulting rotated endpoint feedback appeared (Fig. 1C). Rotation magnitudes varied from -150° to 150° in 30° increments, and were randomized across trials. As seen in Figure 1D, we found a linear relationship between absolute rotation magnitude and RT on the second trial of each pair, when subjects were attempting to counter the observed rotation ( $\mu$  regression coefficient = 0.89,  $p = 0.03$ ).

Based on the findings of Georgopoulos et al. (1989), which showed that an M1 population vector appears to “rotate” while a monkey plans a rotated reach, we reasoned that if we *forced* subjects to move before they are fully prepared, then movements should be made at intermediate angles between the target and fully rotated movement depending on the preparation interval (also see Haith et al., 2015, 2016). In this difficult forced-response-time task, subjects must synchronize the initiation of their movement with the last of four equally-spaced tones (Fig. 2A, see legend and Haith et al., 2015 for further details), and have to execute the movement to an unknown target location in a short time. Critically, the subjects were also simultaneously countering a fixed 90° clockwise rotation. Each subject ( $n = 8$ , subjects all performed the previous task) performed 480 trials with 5 possible RT windows (~300 - 500 ms, see legend), which determined how long they observed a pseudorandomly-located target before they had to rapidly move and attempt to land the rotated cursor on it. To keep subjects on task, ~16% of trials were “catch” trials, where the target appeared at the very end of the RT window (subjects were instructed to reach randomly on such trials).

As predicted, at larger RT windows, subjects' movements increased linearly toward the 90° rotated direction (Fig. 2B). An ANOVA revealed a significant main effect of RT window size on reach angle ( $p < 0.001$ ), and a  $t$ -test revealed significant regression coefficients (RT Window X Reach Angle) as well ( $p < 0.01$ ). Importantly, given that subjects' movements were highly variable given the difficulty of the task, one interpretation could be that our result is due to variance changes across the RT windows. This would suggest that because random movements (which should have a mean reach angle of 0°) are less probable at higher RTs (Haith et al., 2016), a linear trend may emerge in the means, but does not suggest true “mental rotation” of the aiming vector. However, polar histograms plotted in Figure 2C show the hypothesized rotation in action — as the RT window increases, the majority of movements slowly shift toward 90°.

Combined, these results suggest that explicit aiming in VMR may require the mental rotation of an imagined goal location or movement trajectory.



**Figure 1:** (A) Random perturbations in a structure-learning paradigm (Bond & Taylor, SFN 2015). Subjects learned to counter a randomly selected perturbation for 8-trials; this format prevented implicit learning over the course of training. (B) After binning the random rotation magnitudes (and taking their absolute value), a linear relationship was revealed between the size of the rotation and the mean of each subject's median RT over the 7 trials after the first exposure to that rotation ( $\mu$  regression coefficient = 3.57,  $p < 0.001$ ). (C) Our "trial pair" paradigm: Subjects performed 144 trial pairs over 11 rotation magnitudes ( $-150^\circ$  to  $150^\circ$  by  $30^\circ$  increments). On the first trial of a pair ("learn", blue target), subjects reached directly to the target to observe the rotation. On the second trial ("probe", red target), subjects attempted to counter the rotation. The target appeared in one of 4 random locations, and rotation magnitudes were randomized across subjects. (D) average of subjects' median RTs as a function of rotation magnitude on the probe trials. As the rotation magnitude increased, so did RT ( $\mu$  regression coefficient = 0.89,  $p = 0.03$ ).

**Figure 2:** (A) The Forced RT task. This task was modeled after that used by Haith et al., (2015, 2016). Subjects synchronized their movement initiation with the 4th of 4 equally spaced tones (with 100 ms of cushion). The target appeared in one of 12 locations at some delay after the 3rd tone. The resulting RT windows, for subjects to plan their movements in, were one of 5 values between  $\sim 300$  ms and 500 ms (with  $\sim 16\%$  0ms catch trials). The lower window value ( $\sim 300$ ms) was determined for each subject by looking at their mean RTs in the trial pair task (see above) and subtracting 200 ms. (If their mean RT was higher than 500 ms, a default 300-500ms window range was used.) Subjects were explicitly instructed about the  $90^\circ$  clockwise rotation on the cursor, and were told to try and counter it every trial. (B) Hand angle as a result of the length of the RT window. As predicted, reach angles (all angles were rotated to  $0^\circ$ ) relative to the target location increased linearly as a function of the size of the RT window ( $p < 0.01$ ), similar to what was observed in classic mental rotation, and the VMR mental rotations in Figure 1. (C) Polar histograms of reach angles over the 5 RT windows. Bar length represents the frequency of a given reach angle across all subjects. Each panel shows the distribution of reach angles at each RT window. As shown, movements are noisy in the smallest window (subjects were indeed instructed to reach randomly if they didn't notice the target in time, and fewer trials were successful); however, the data show that reach angles are gradually rotated toward  $90^\circ$  as the RT window increases, supporting the mechanism offered by Georgopoulos et al. (1989).

