

RESEARCH ARTICLE | *Control of Movement*

Visuomotor learning is dependent on direction-specific error saliency

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Jiang W, Yuan X, Yin C, Wei K. Visuomotor learning is dependent on direction-specific error saliency. *J Neurophysiol* 120: 162–170, 2018. First published March 28, 2018; doi:10.1152/jn.00787.2017.—People perceive better in cardinal directions compared with oblique ones. This directional effect, called oblique effect, has been documented in perception studies for a long time. However, typical motor studies do not differentiate learning in different directions. In this study we identify a significant directional effect in motor learning using visuomotor rotation paradigms. We find that adaptation to visual perturbations yields more savings when both initial learning and relearning are performed in cardinal directions than in oblique directions. We hypothesize that this directional effect arises from relatively higher error saliency in cardinal directions. Consistent with this hypothesis, we successfully increased savings in the oblique directions, which showed no saving effect before, by enhancing the error saliency with augmented visual feedback during learning. Our findings suggest that movement direction plays an important role in motor learning, especially when learning signals are direction specific. Our results also provide new insights about the role of motor errors in the formation and retrieval of motor memory and practical implications for promoting learning in motor rehabilitation and athletic training.

NEW & NOTEWORTHY People perceive better when the stimulus is in cardinal directions than in oblique directions. Whether a similar directional effect exists in motor learning is unknown. Using a motor learning paradigm, we show that people relearn to compensate for a previously encountered perturbation faster when they move in cardinal directions than when they move in oblique directions. Further experimentation supports that this motor directional effect likely results from better sensory saliency of motor errors in cardinal directions.

error saliency; motor adaptation; motor generalization; oblique effect; visuomotor rotation

INTRODUCTION

People move in three-dimensional space. Although the vertical direction has been a special direction for motor control given its association with gravity (Senot et al. 2012; Zago et al. 2004), whether other directions make a difference in neural control of movements remains unclear. For motor performance, there is directional effect for planar reaching movements. For example, people have a tendency to move faster in

the directions with low inertia of the upper limb, i.e., directions more perpendicular to the forearm, than in the directions with high inertia, i.e., directions more parallel to the axis of the forearm (Gordon et al. 1994; van Beers et al. 2004). When pointing to memorized targets, people tend to direct their movements away from cardinal and toward oblique directions (Smyrnis et al. 2007; van Beers et al. 2004). In contrast to these motor control studies, studies on motor learning have not identified a similar directional effect. Previous motor learning studies either opted to focus on testing movements in oblique directions (Krakauer et al. 2000; Pine et al. 1996; Sainburg and Wang 2002) or opted to treat oblique and cardinal directions without distinctions (Brashers-Krug et al. 1996; Krakauer et al. 2005; Shadmehr and Holcomb 1997; Taylor et al. 2014; Tong et al. 2002). When learning to counter a visuomotor perturbation is specifically examined between oblique and cardinal directions, researchers have reported that learning is similar across different Cartesian directions (Mattar and Ostry 2007).

However, the difference between oblique and cardinal directions, called oblique effect, has been investigated in the realm of perception for a long time. In visual perception, people make less discrimination error when the direction of stimulus is cardinal rather than oblique (Berkley et al. 1975; Taylor 1963; Vogels and Orban 1985). This effect presumably results from the asymmetric responsiveness of cortical neurons to oblique and cardinal directions, especially in the primary visual cortex (V1; Furmanski and Engel 2000; Li et al. 2003; Maffei and Campbell 1970). Similarly, for haptic perception, when people haptically perceive the direction of a target rod and then match it with the direction of a comparison rod, they perform more accurately when the target rod is in the cardinal direction than when it is in the oblique direction (Appelle and Countryman 1986; Gentaz and Hatwell 1996; Lechelt et al. 1976; Luyat et al. 2001). These findings imply that people perceive the stimulus better in the cardinal direction than in the oblique direction.

We hypothesize that motor learning might show a similar directional effect if learning is critically dependent on the saliency of perceptual signals. To test our hypothesis, we examine the generalization of visuomotor rotation adaptation using savings as the learning metric (Krakauer et al. 2005; Yin et al. 2016). Savings refers to the phenomenon that relearning is faster than the initial learning. It has been established that savings is sensitive to error feedback; e.g., it is prevented when

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large noticeable errors are absent during initial learning (Herzfeld et al. 2014; Morehead et al. 2015). Thus we hypothesize that savings in cardinal directions, which is presumably associated with better discrimination of directional errors, should be larger than that in oblique directions. We find that savings is indeed generalized better when both the initial learning and relearning are in cardinal directions than when in oblique directions. In support of the intermediate role of error saliency for this directional effect, our further experimentation provides augmented feedback for the learning in oblique directions and successfully enables the generalization of savings that is otherwise not generalizable.

MATERIALS AND METHODS

Participants

A total of 192 right-handed participants (140 women, age: 20.55 ± 2.12 yr, mean $\pm$ SD) were recruited and randomly assigned to 16 experimental groups ($n = 12$ per group). All participants were new to the experimental task, naive to the purpose of the study, provided written informed consent before participating, and were paid for their time. All experimental protocols were approved by the Institutional Review Board of Peking University.

Experimental Setup

The experimental setup had been used in our previous research (He et al. 2016; Wei et al. 2014; Yin and Wei 2014; Yin et al. 2016). Participants sat in front of a table and slid their right index fingertips on the desktop (Fig. 1A). They were instructed to make straight, center-out shooting movements toward a target as accurately as possible without corrections. The movement of the index fingertip was measured at 200 Hz by a motion capture system (Codamotion; Charnwood Dynamics, Rothley, UK). Visual feedback was provided through a mirror-projection system (LCD projector; Acer P1270) with a display frequency of 75 Hz. View of the hand and arm was occluded by a semi-silvered mirror placed horizontally at the chest level.

Procedure

Before each trial, the participant held her or his index fingertip on a starting position, which was marked by a 4-mm (8.8 pixel) plastic disk glued on the desktop. This starting position was at the center of

the workspace and aligned with the midline of the seated participant. The disk provided tactile cues to facilitate the participant to return her or his unseen index finger back to the starting position after each trial. Meanwhile, the starting position was also shown as a yellow cross (6 pixels per line; 1-mm distance equals 2.2 pixels in our visual display) at the same position as the disk. The visual feedback of the index finger, represented as a green disk with a 3-pixel diameter, was visible only within 4 mm around the starting position. After the finger remained at the starting position for 1 s, the yellow cross disappeared, a visual target appeared, and a beep sound was played to trigger the participant to move. The visual target, presented as a white disk with a 6-pixel diameter, was displayed 70 mm from the starting position. The straight-ahead target was defined as a 0° target, and the rightward target was defined as a 90° target. Thus the direction angle increased clockwise from straight ahead, ranging from 0° to 360° . The participant was instructed to make a fast, straight movement to accurately hit the target with the cursor. In our instruction before the experiment, we did not mention any explicit strategy that could be used in the task. However, the use of a strategy was not prohibited. Once the movement amplitude exceeded 70 mm, a different beep was played to signal the end of the trial. If the distance between the cursor and the target was less than 6 pixels, the color of the target turned from white to red to signal a target hit. The accumulative number of target hit was displayed at the top-right corner of the screen to motivate participants. A low-pitched tone warned the participant if he or she moved too fast or too slowly (movement time <100 or >400 ms), although these trials were not repeated. Participants met this speed requirement for the majority of trials ($93.26 \pm 8.99\%$ across participants, mean $\pm$ SD).

The learning was examined with typical visuomotor rotation paradigms. The experiment was organized as five consecutive epochs: familiarization, baseline, first learning, washout, and second learning. In the familiarization epoch, participants performed 40 trials without visual perturbations. There were 20 trials for each learning direction, and their order was randomized across trials. Veridical cursor feedback was provided all the time. In subsequent epochs, the cursor feedback was only briefly shown for 500 ms in the form of end-point cursor feedback. The baseline epoch was identical to the familiarization epoch except that end-point feedback was used. This epoch established the performance baseline before adaptation. In the first learning epoch, a visuomotor rotation was introduced, and the end-point cursor feedback was rotated 30° counterclockwise from the actual finger position. After 80 learning trials, we returned participants' performance to baseline by asking them to move for 40 trials with veridical feedback in the washout epoch. Finally, in the second learning epoch, participants relearned the 30° rotation in the same target direction or a new one for 80 trials. As our critical measure, savings was defined as the difference in learning rate between the first and the second learning epochs.

Experimental Design

Experiment 1 (generalization in oblique directions). Experiment 1 was designed to assess how generalization varies as a function of the angular separation between the first and the second learning directions. Critically, both directions were oblique (Fig. 1B, Oblique-Both groups). Separate groups of participants shared the same second learning direction (320°), but their first learning directions varied (320° , 5° , 50° , 95° , or 140°). Thus between-epoch angular separation for these five participant groups was 0° , 45° , 90° , 135° , and 180° , respectively.

Experiment 2 (generalization in cardinal directions). Inspired by perceptual oblique effect, we predicted that if a similar directional effect exists in motor learning, moving in cardinal directions should lead to a larger amount of generalization than moving in oblique directions. To test this hypothesis, we rotated the first and/or the second learning directions to cardinal directions while keeping their

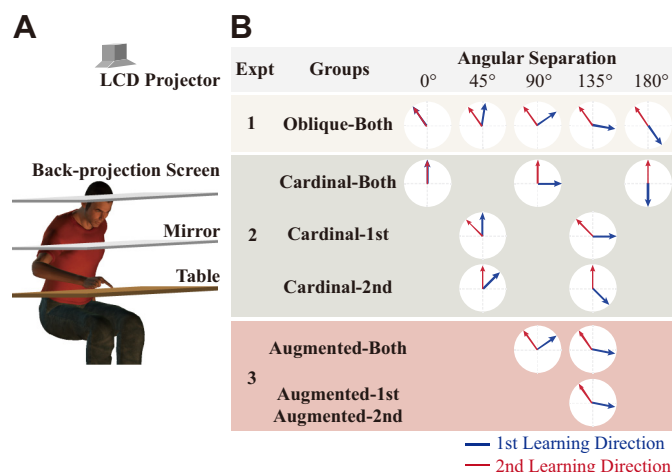


Fig. 1. Experimental setup and designs. A: experimental setup. B: experimental designs. Blue and red arrows indicate target directions for the first and the second learning epochs, respectively. Expt, experiment.

angular separations unchanged from those in *experiment 1* (Fig. 1B). Three cardinal groups (Cardinal-Both) first learned in one of three cardinal directions (0°, 90°, or 180°) and relearned in the same cardinal direction (0°). Thus their generalization was examined with the angular separation of 0°, 90°, or 180°, respectively. Two cardinal groups (Cardinal-2nd) performed their first learning in oblique directions (45° or 135°) and second learning in a cardinal direction (0°). Thus these two groups generalized their learning to angular separations of 45° and 135°, respectively. For these two angular separations, learning in cardinal directions was only for the second learning epoch. To examine whether learning in cardinal directions in the first learning epoch will make a difference, we recruited two additional groups (Cardinal-1st) to perform initial learning in cardinal directions (0° or 90°) and relearning in an oblique direction (315°). Note that these two Cardinal-1st groups, similarly to Cardinal-2nd groups, also generalized with angular separations of 45° and 135°, respectively.

Experiment 3 (generalization with enhanced error saliency). If the directional effect results from varying levels of error saliency in different movement directions, providing extra visual cues to enhance error saliency should facilitate generalization. First, we tested this hypothesis by using the angular separation of 135° that was associated with minimum generalization as shown in both *experiment 1* and 2 (see Figs. 3 and 4). A solid white straight line (1 pixel) was displayed throughout the trial, connecting the starting point to the target. With this augmented feedback, the end-point feedback and the directional error resulting from visuomotor rotation were more salient. Participants were able to compare their end-point feedback (a briefly shown cursor) directly with the straight line, which signified the desired cursor direction. In contrast, previous conditions only provided end-point cursor feedback whose perturbed location might be less evident as caused by a rotated perturbation. For different groups of participants, this augmented feedback was presented only during the first learning epoch (Fig. 1B, 135° Augmented-1st group), only during the second learning epoch (135° Augmented-2nd group), or during both the first and the second epochs (135° Augmented-Both group). For a 90° angular separation, we found that moving in cardinal directions led to substantial savings, whereas moving in oblique directions led to none (see Fig. 4). If this effect was caused by better error saliency in cardinal directions, we would expect to find the same substantial savings when we provided augmented feedback for the 90° condition in *experiment 1*. We thus recruited another 90° Oblique-Both group (as in *experiment 1*) and provided the augmented feedback during both the first and the second epochs (90° Augmented-Both group).

Data Analysis

The learning of visuomotor rotation was quantified by the directional error of shooting movement. The error was defined as the angular difference between the desired direction and the actual movement direction, estimated by the vector from the starting position to the end point of actual movement. The desired direction was the target direction in the baseline and washout epochs while it was rotated 30° clockwise during visuomotor rotation in the two learning epochs. The average movement direction for the last 10 trials in the baseline epoch was estimated as the baseline performance for each participant. This bias was subtracted from the learning data before savings was computed. The learning rate was estimated as the average directional error over trials 2–9 for the two learning epochs separately (Krakauer et al. 2005; Yin et al. 2016). The average error was divided by the desired rotation angle of 30°, yielding a learning percentage. This learning rate measure was more robust than that estimated from the exponential fitting of individual learning curves (Morehead et al. 2015). Savings was computed as the difference in learning rates between the first and the second learning epochs. We also quantified the extent of learning during the first learning epoch as the difference between the error in the first trial and the average error over the last 10 trials.

Between-condition comparisons of learning rate, learning extent, and savings were performed by one-way ANOVAs. Post hoc comparisons between multiple groups were conducted with Bonferroni corrections. The homoscedasticity and normality assumptions were examined before ANOVAs were performed. All dependent variables satisfied these assumptions unless otherwise mentioned. Welch's ANOVA was used if the homoscedasticity assumption was not satisfied. To detect generalization, savings of each group was tested against zero by a two-sided, one-sample *t*-test. Significance level was set at $\alpha = 0.05$. As robust tests, the bootstrapped one-way ANOVAs (Wilcox 2012) and the bootstrapped two-sided, independent-samples *t*-tests were also performed for corresponding comparisons. The number of bootstrap samples was set to be 1,000, and the confidence interval was 95%. We confirmed that the robust tests with bootstrapping yielded testing results similar to those of normal ANOVAs; thus only the results of the latter are reported. All analyses were performed with MATLAB (The MathWorks, Natick, MA), R (<https://www.r-project.org>), and SPSS version 19 (IBM, Somers, NY).

RESULTS

All experiments shared the same procedures: participants learned visuomotor rotation at one direction, washed out their learning at that direction, and relearned the same rotation at the same or a different direction. We assessed their directional generalization as a function of angular separation. Critically, directions for both the first and the second epochs were oblique in *experiment 1*, and one or both learning directions were cardinal in *experiment 2*. The differences between these two experiments served as evidence of directional effect in motor learning. We further hypothesized that the advantage of cardinal directions lies in its association with direction-specific saliency of movement errors. This hypothesis was tested in *experiment 3*, where we provided extra directional visual information for the first learning and/or the second learning epochs.

Experiment 1

This experiment examined directional generalization when both the first learning direction and the second learning direction were oblique. With the group of angular separation of 0° taken as an example, participants started the experiment with small baseline errors (Fig. 2A). They produced large directional errors when the visuomotor rotation was introduced in the first learning epoch. They learned to counter the perturbation as shown by a gradual reduction of directional errors over the subsequent trials. In the washout epoch, when the rotation was unexpectedly removed, they yielded negative errors as a signature of aftereffects, and again, they reduced the error. Importantly, when learning the rotation for the second time, they exhibited faster learning than the first time. That is, subjects in this group exhibited the typical saving effect.

This saving effect was reduced when the angular separation between the first learning direction and the second learning direction increased when five groups of participants were compared (Fig. 2B). First, we confirmed that all participant groups had similar learning rates during the first learning epoch ($F_{4,55} = 0.838$, $P = 0.507$, one-way ANOVA; Fig. 3A). However, savings, the learning rate difference between the first and the second learning epochs, exhibited group differences. The savings were $32.06 \pm 4.70\%$, $20.34 \pm 7.88\%$, $2.78 \pm 6.60\%$, $3.08 \pm 5.65\%$, and $13.72 \pm 2.52\%$ for the 0°, 45°, 90°, 135°, and 180° angular separations, respectively (means $\pm$ SE; $F_{4,55} =$

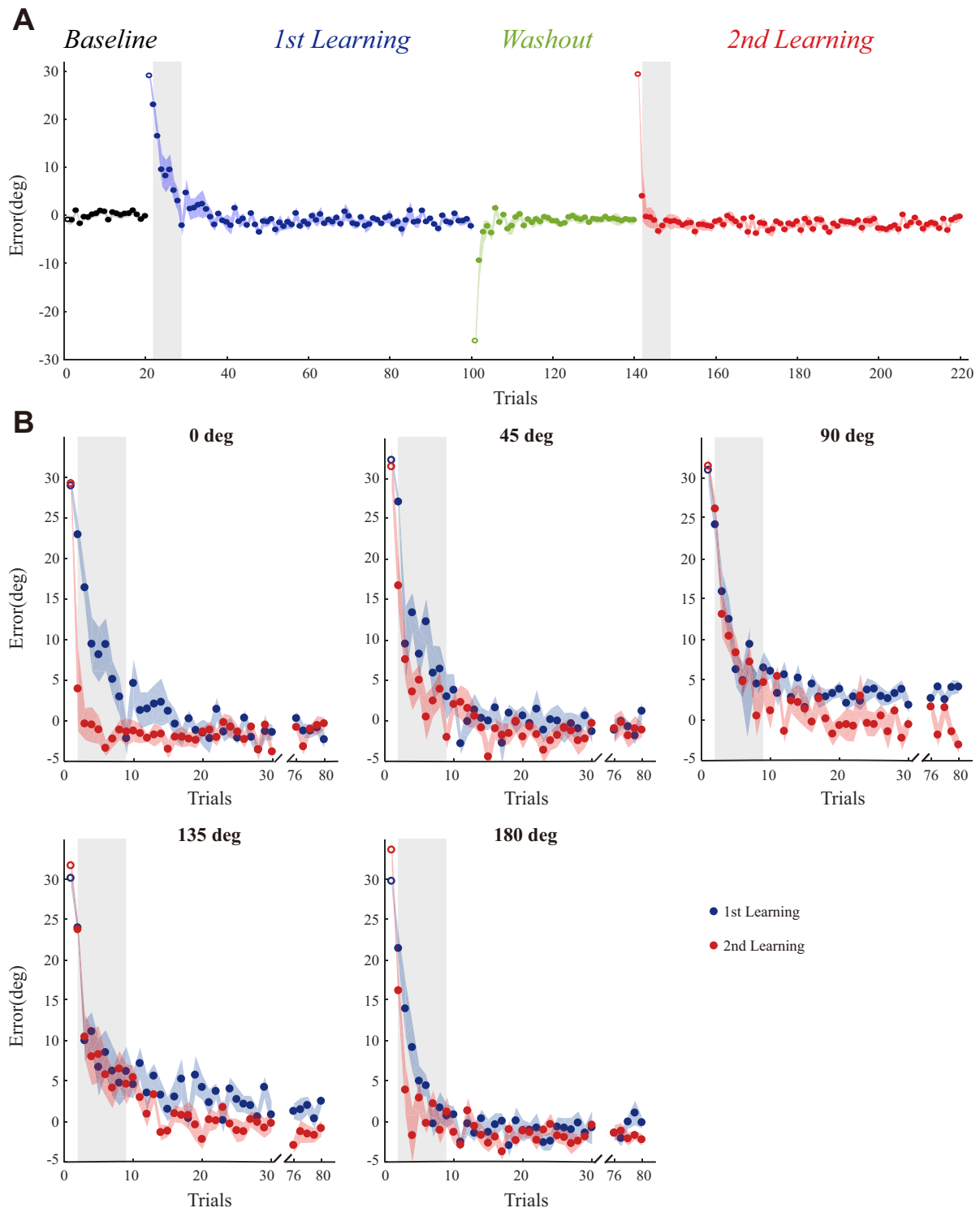
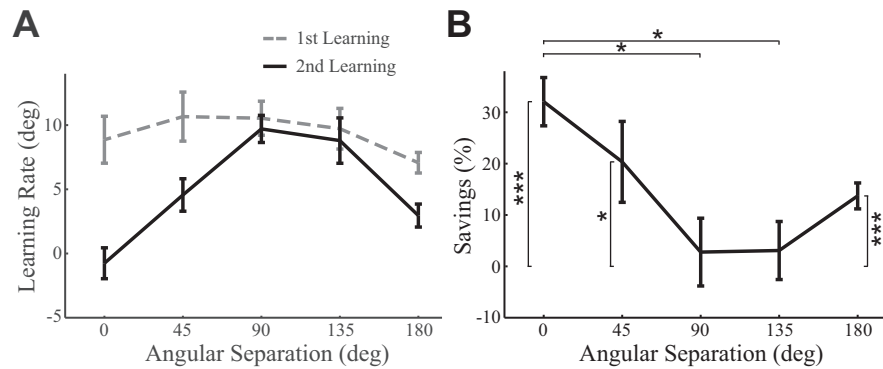


Fig. 2. Learning performance in *experiment 1*. *A*: exemplar results from the Oblique-Both group with 0° angular separation. Trial-by-trial changes of directional errors are shown with different trial epochs represented in different colors. Circles denote means and shaded areas denote SE. A positive error means that the direction of the subject's actual movement is counterclockwise to the desired direction. The first trial in each epoch is shown as an open circle. Gray boxes highlight trials 2–9 in the first and second learning epochs where learning rate is estimated. Note that learning is faster in the second learning epoch than in the first epoch. *B*: performance during the first and second learning epochs, shown separately for the Oblique-Both groups with 5 different angular separations.

4.217, $P < 0.01$, partial $\eta^2 = 0.235$, one-way ANOVA; Fig. 3*B*). Savings were significantly above 0 for two small angular separations ($P < 0.001$ and 0.05 for the 0° and 45° groups, respectively; t -test) but not significantly different from 0 for two larger angular separations ($P = 0.695$ and 0.612 for the

90° and 135° groups, respectively; t -test). This seemingly decreasing trend of savings did not extend to 180°, which showed significant savings ($P < 0.001$, t -test). Post hoc pairwise comparisons confirmed this trend: savings in the 90° and 135° groups were significantly lower than in the 0° group ($P <$

Fig. 3. Learning rate and savings in *experiment 1*. *A*: learning rate plotted as a function of angular separation during the first (gray dashed line) and second (black solid line) learning epochs. *B*: savings plotted as a function of angular separation. * $P < 0.05$; *** $P < 0.001$.



0.05 for both comparisons). Thus, when both the first and the second learning directions were oblique, savings generalized poorly to directions with large angular separations, except for the opposite direction of 180°.

Experiment 2

To examine whether generalization will be affected by learning directions, seven groups of new participants were tested with the same angular separations as in *experiment 1*. The critical manipulation was that one or both directions for the first and the second learning epochs were cardinal. These Cardinal groups achieved similar learning rates during the first learning epoch ($F_{6,77} = 1.308$, $P = 0.264$, one-way ANOVA), which were also comparable to those of previous Oblique-Both groups in *experiment 1* ($F_{11,132} = 1.063$, $P = 0.396$, one-way ANOVA). Among all 12 groups in *experiment 1* and 2, whether the first learning direction was oblique or cardinal did not significantly affect learning rate or learning extent during the first learning epoch (learning rate: $F_{1,142} = 0.009$, $P = 0.923$; learning extent: $F_{1,142} = 0.008$, $P = 0.929$; one-way ANOVA).

The direction affected the generalization of savings to varying degrees when the angular separations were different. One-way ANOVAs with direction (cardinal vs. oblique directions) as a between-subject factor were performed for each of five angular separations (0°, 45°, 90°, 135°, 180°). When the angular separation was 0°, the savings of Cardinal-Both and Oblique-Both groups were significantly above 0 ($P < 0.01$ and 0.001, respectively, t -test) without significant group difference ($F_{1,22} = 0.296$, $P = 0.592$, one-way ANOVA; Fig. 4). When the angular separation was 45°, the savings achieved by the Cardinal-1st, Cardinal-2nd, and Oblique-Both groups were all significantly above 0, and they did not differ from one another either ($P < 0.01$, 0.01, and 0.05, respectively, t -tests; $F_{2,33} = 0.145$, $P = 0.865$, one-way ANOVA). However, direction affected generalization significantly when the angular separation was 90° ($F_{1,22} = 12.294$, $P < 0.01$, partial $\eta^2 = 0.358$, one-way ANOVA): savings were significantly above 0 for the Cardinal-Both group ($P < 0.001$, t -test) but not significantly different from 0 for the Oblique-Both group ($P = 0.695$, t -test). The directional effect was absent for the 135° and 180° angular separations (135°: $F_{2,33} = 0.203$, $P = 0.817$, one-way ANOVA; 180°: $P < 0.05$, Levene's F -test, $F_{1,14.334} = 0.842$, $P = 0.374$, Welch's ANOVA). In fact, there were no savings for all the groups with 135° angular separation ($P = 0.162$, 0.627, and 0.612 for the Cardinal-1st, Cardinal-2nd, and Oblique-Both groups, respectively; t -test). There were savings for two groups with 180° angular separation, though ($P < 0.05$ and 0.001 for

the *Cardinal-Both* and *Oblique-Both* groups, respectively; t -test). In sum, we found significantly more generalization for the angular separation of 90° during movement in cardinal directions than movement in oblique directions, and this directional effect was absent for other angular separations.

Experiment 3

Experiment 3 examined whether upregulation of error saliency could lead to more generalization of motor learning. First, we chose the same setup as for the 135° Oblique-Both group in *experiment 1*, which experienced both learning epochs in oblique directions. It was also the condition with the least generalization. Three groups of participants were tested with augmented visual feedback in either the first learning direction (135° Augmented-1st) or the second learning direction (135° Augmented-2nd), or in both directions (135° Augmented-Both). The 135° Oblique-Both group in *experiment 1* served as the control group. All four groups started off with similar learning rates during the first learning epoch ($F_{3,44} = 0.829$, $P = 0.485$, one-way ANOVA). Similarly to *experiment 2*, whether augmented feedback was provided during the first learning epoch did not significantly affect the rate or extent of initial learning (learning rate: $F_{1,46} = 0.303$, $P = 0.585$; learning extent: $F_{1,46} = 1.809$, $P = 0.185$; one-way ANOVA).

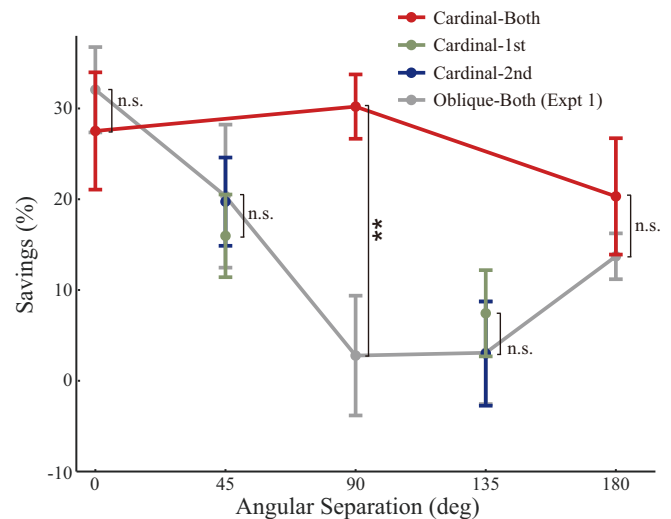


Fig. 4. Savings estimated from *experiment 1* and 2 are plotted as a function of angular separation. Groups are shown separately depending on whether cardinal or oblique directions were used during learning. ** $P < 0.01$. n.s., Not significant.

Providing augmented feedback indeed facilitated generalization. The savings were $3.08 \pm 5.65\%$, $2.56 \pm 4.14\%$, $10.12 \pm 3.10\%$, and $21.81 \pm 4.30\%$ for the 135° Oblique-Both, 135° Augmented-2nd, 135° Augmented-1st, and 135° Augmented-Both groups, respectively ($F_{3,44} = 3.822$, $P < 0.05$, partial $\eta^2 = 0.207$, one-way ANOVA; Fig. 5A). Savings were not significantly different from 0 for the 135° Oblique-Both and 135° Augmented-2nd groups ($P = 0.612$ and 0.566 , respectively; t -test). However, the 135° Augmented-1st group and the 135° Augmented-Both group exhibited significant savings ($P < 0.01$ and 0.001 , respectively; t -test). Post hoc pairwise comparisons indicated that savings for the 135° Augmented-Both group was significantly larger than that for the 135° Oblique-Both and 135° Augmented-2nd groups ($P < 0.05$ for both comparisons). Additionally, we also compared these enhanced savings with that for the 0° Oblique-Both group in *experiment 1*, which yielded the maximum savings for a condition with two oblique learning directions. Although there was significant group difference ($F_{4,55} = 7.532$, $P < 0.001$, partial $\eta^2 = 0.352$, one-way ANOVA), post hoc pairwise comparison showed that savings for the 135° Augmented-Both group was indistinguishable from that for the 0° Oblique-Both group ($P = 1.000$). Savings for the 135° Oblique-Both, 135° Augmented-2nd, and 135° Augmented-1st groups were significantly smaller than for the 0° Oblique-Both group ($P < 0.001$, 0.05 , and 0.001 , respectively). Therefore, presenting augmented feedback during both the first and the second learning epochs could enable substantial savings for 135° angular separation, which otherwise did not show a saving effect.

Second, we also provided augmented feedback when participants moved in oblique directions for both learning epochs with 90° angular separation. This condition previously did not show any generalization of savings (the 90° Oblique-Both group in *experiment 1*), and simply moving in cardinal directions for both learning epochs (the 90° Cardinal-Both group in *experiment 2*) led to significantly more generalization of savings. We found that augmented feedback indeed improved the generalization ($P < 0.001$, t -test). In fact, the generalization was improved to a level similar to that of the 90° Cardinal-Both group in *experiment 2*. One-way ANOVA on savings showed significant group difference among the 90° Oblique-Both, 90° Cardinal-Both, and 90° Augmented-Both groups ($F_{2,33} = 8.138$, $P < 0.01$, partial $\eta^2 = 0.330$, one-way ANOVA; Fig. 5B). Post hoc pairwise comparisons indicated that savings for the 90° Augmented-Both and 90° Cardinal-Both groups were significantly larger than for the 90° Oblique-Both group ($P <$

0.05 and 0.01 , respectively), but savings for the former two conditions did not differ from one another ($P = 1.000$). Thus, consistent with the 135° condition, providing augmented feedback during both the first and the second learning epochs could also evoke substantial savings for the 90° condition. The effect of presenting augmented feedback during both learning epochs appeared comparable to that of moving in cardinal directions.

DISCUSSION

Controlling movement in different Cartesian directions has been investigated for a long time. Most studies examined how motor control differs in different movement directions under the influence of mechanical properties of the limb (Gordon et al. 1994; van Beers et al. 2004) or gravitational force (Senot et al. 2012; Zago et al. 2004). In contrast, in the realm of motor learning, moving in different directions in the Cartesian space has been treated equivalently (Brashers-Krug et al. 1996; Krakauer et al. 2000, 2005; Mattar and Ostry 2007; Pine et al. 1996; Sainburg and Wang 2002; Shadmehr and Holcomb 1997; Taylor et al. 2014; Tong et al. 2002). In the present study, we have demonstrated that the direction of reaching movement in the horizontal plane does make a difference for visuomotor learning. With an angular separation of 90°, the amount of generalization significantly increases when two learning directions are cardinal compared with when both of them are oblique. We postulate that this directional effect likely results from enhanced error saliency associated with moving in cardinal directions and find that generalization can be improved if augmented feedback is provided at oblique directions.

Previous studies on motor generalization of adaptation have not reported any directional effect (Krakauer et al. 2000; Mattar and Ostry 2007; Pine et al. 1996; Sainburg et al. 1999; Taylor et al. 2013). This lack of effect may be due to the fact that these studies probed generalization by aftereffects. In contrast, our study used savings as the metric for generalization (Yin et al. 2016). Manifested as faster learning during a relearning epoch, savings represent a stable, long-term learning effect that is resilient to washout and deadaptation brought by moving in unperturbed contexts (Krakauer et al. 2005; Yin et al. 2016). Critically, savings are measured when the original learning signal (i.e., visual error) is provided. Thus savings might be more prone to the subtle effect of direction-specific error saliency. In contrast, aftereffects are a transient learning effect that is measured immediately after adaptation without

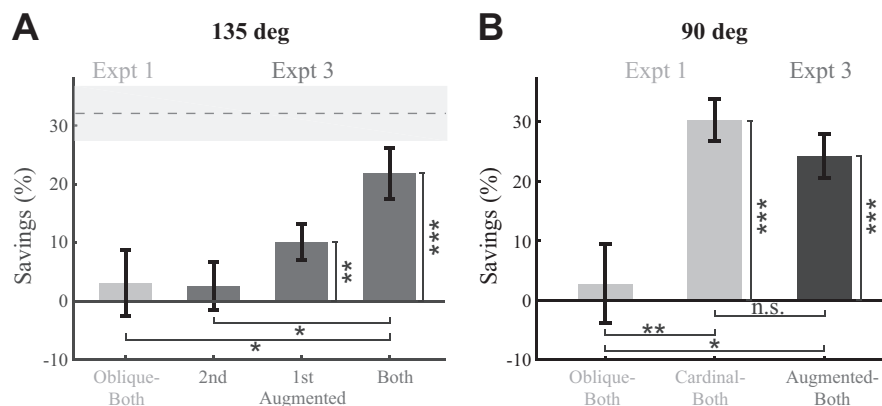


Fig. 5. Savings estimated from *experiment 3*. A: savings for the 3 Augmented groups (dark gray bars) with 135° angular separation whose learning was aided by extra visual cues. To highlight the effect of augmented feedback, savings observed in 2 groups from *experiment 1* are displayed: light gray bar is the savings estimated from the 135° Oblique-Both group, and the horizontal dotted line and gray shaded area represent the mean and SE for the 0° Oblique-Both group, respectively. B: savings for the 90° Augmented-Both group whose learning was aided by extra visual cues. To highlight the effect of augmented feedback, savings observed in 2 groups from *experiments 1* and *2* are displayed: *left* and *middle* gray bars are the savings estimated from the 90° Oblique-Both and 90° Cardinal-Both groups, respectively. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. n.s., Not significant.

visual feedback. Given that this directional effect in motor learning is arguably a visual phenomenon similar to the visual oblique effect, it is not surprising that generalization studies based on aftereffects failed to report any directional effect.

On the other hand, we cannot rule out the possibility that the failure to report directional effect in previous studies might be a result of limited effect size for learning in the cardinal direction. In our experiments, we failed to observe directional effect for 45° and 135° in *experiment 2* (Fig. 4). Of note, these two conditions only have one cardinal direction, either for the first or the second learning epoch. In contrast, we found a significant directional effect in the 90° condition, which involves moving in cardinal directions for both learning epochs. Thus the directional effect may be dose dependent. This speculation is supported by findings in *experiment 3*: the effect of augmented feedback on the generalization of savings is small when the extra visual cue is provided only for one learning epoch, but the effect becomes larger and reaches the significance level when the extra visual cue is provided for both epochs. In sum, the effect of moving in cardinal directions appears to be dose dependent, and its effect size is limited. Whether this limited effect size also holds for learning that is assessed by aftereffects is in need of further investigation.

We argue that both movement direction and angular separation, a traditional tuning parameter for the generalization of learning, contribute to the generalization of visuomotor rotation. However, the directional effect is subtle compared with the effect of angular separation. First, for small angular separations of 0° and 45°, where generalization is already large for oblique directions, moving in the cardinal direction does not further enhance savings. Second, for large angular separation of 135°, where savings are effectively nonexistent (Yin et al. 2016), moving in the cardinal direction does not enhance savings either, no matter whether the cardinal direction is involved in the first or the second learning epoch. Last, the generalization to 180° separation is also not affected by direction. The limited demonstration of this directional effect suggests that generalization of visuomotor rotation is mainly determined by the amplitude of angular separation (Donchin et al. 2003; Krakauer et al. 2000; Pine et al. 1996; Sainburg et al. 1999; Shadmehr 2004; Taylor et al. 2013; Yin et al. 2016).

Our findings are consistent with two prevailing accounts of savings. A series of work from Taylor and colleagues suggests that savings results from learning of an explicit strategy, which can be quickly recalled and deployed during relearning (Haith et al. 2015; Huberdeau et al. 2015; Morehead et al. 2015; Taylor et al. 2014). On the other hand, Shadmehr and colleagues suggest that the motor system might maintain a memory of experienced sensory prediction error, which can be recalled to facilitate relearning (Herzfeld et al. 2014). Both accounts emphasize the role of large, noticeable errors, which are prerequisite for the saving effect (Herzfeld et al. 2014; Morehead et al. 2015). In our *experiments 2* and *3*, we found evidence that moving in cardinal directions or providing augmented feedback leads to more generalization of savings. Given the well-documented visual oblique effect (Berkley et al. 1975; Taylor 1963; Vogels and Orban 1985), we postulate that moving in cardinal directions might be associated with better processing of error information. This enhanced error saliency may benefit the formation of a cognitive strategy during the first learning epoch as well as the recall of the

strategy during the second learning epoch. It could also benefit the encoding and retrieval of error information, which have been argued to underlie the saving effect (Herzfeld et al. 2014). We cannot refute either of the two accounts, but our findings do highlight the role of direction-specific error saliency in savings.

By providing augmented feedback, we enable the generalization of savings in oblique directions. When people make hand movements in a typical virtual reality setup, they have large uncertainty about where the hand is because veridical visual feedback of the hand is only intermittently shown (Ma-Wyatt and McKee 2007; Rossetti et al. 1994). When adapting to visuomotor rotation, participants only see the cursor at the end of a trial, and they need to correct for this novel visuomotor transformation. This rotated end-point feedback might have its inherent ambiguity: it could be caused by a lateral deviation from the target or a direction rotation, or a combination of both. We postulate that presenting a straight line along the desired cursor direction helps to resolve the ambiguity of the end-point error and thus enhances error saliency.

The error-saliency account for motor directional effect is in line with extensive findings in perception studies that have found higher sensitivity to directional errors in cardinal directions than in oblique ones (Appelle and Countryman 1986; Berkley et al. 1975; Gentaz and Hatwell 1996; Lechelt et al. 1976; Luyat et al. 2001; Taylor 1963; Vogels and Orban 1985). Adaptation of visuomotor rotation is specifically driven by sensory prediction error of directions, i.e., the discrepancy between the anticipated movement direction and the perceived movement direction (Izawa and Shadmehr 2011; Shadmehr et al. 2010; Tseng et al. 2007). Previous studies have established that uncertainty of error feedback slows down adaptation (Burge et al. 2008; He et al. 2016; Körding and Wolpert 2004; Wei and Körding 2010). In contrast, providing more sensory feedback with continuous cursor display, as compared with intermittent display at the end of the movement, would lead to more adaptation (Barkley et al. 2014) and generalization (Shabbott and Sainburg 2010). Thus visuomotor adaptation and generalization are sensitive to the quality of visual errors, and this type of error-based learning is closely related to the cerebellum (Shadmehr 2004). Of note, we did not find a directional effect in terms of learning rate or extent during the first learning epoch (*experiment 2*). Providing augmented feedback (*experiment 3*) does not change initial learning either. The observed directional effect is specifically tied to the saving effect during relearning, a long-term effect of adaptation. We speculate that this result might again reflect that the size of directional effect is small. Furthermore, the learning of a visuomotor rotation is simple given people can reach their learning plateaus within ~20 trials. Both factors, small effect size and efficient initial learning, may contribute to the observed null effect for initial learning.

We found that the nervous system appears to treat the 180° condition differently from other large angular separations during the generalization of visuomotor rotation. Previous studies on visuomotor rotation have shown that generalization becomes zero for large angular separations exceeding a certain threshold. The threshold approximately amounts to 45° if measured by trial-by-trial generalization function (Tanaka et al. 2009) or 90° if measured by aftereffects (Krakauer et al.

2000; Mattar and Ostry 2007; Pine et al. 1996). Thus the 180° condition should theoretically have zero generalization. However, a close inspection of previous reports on aftereffects reveals a peculiar increase of generalization for 180° (e.g., Fig. 3 in Pine et al. 1996 and Fig. 6A in Krakauer et al. 2000), although this small effect has been largely overlooked. Our *experiment 1* and 2 showed significant generalization of savings to 180° no matter whether learning directions were oblique or not. Thus the 180° angular separation appears to be distinct from other angles that constitute a monotonically decreasing generalization function. It is worth noting that for visuomotor rotation, both visual perturbation and desired corrective movement are mirror copies of each other in the two learning epochs in the condition of 180° angular separation. This spatial symmetry might facilitate the recall of acquired strategy and/or error memories and, subsequently, lead to better savings. The symmetry might also facilitate the generalization by possible learning from the returning movement, i.e., in a typical visuomotor rotation paradigm, when participants receive cursor feedback when they return the hand to the starting position. Although this feedback is veridical, participants might also benefit from it if they compare it with the rotated feedback at the end of the reach. Coincidentally, the returning movement of the first learning epoch has the same direction as the reaching movement in the second learning epoch, where the generalization (evaluated by savings or aftereffects) at 180° is tested. Thus this similarity might benefit the generalization at 180°, a possibility that shall be investigated in the future.

Enhancing error saliency for better motor learning has been documented for long in the areas of sports training and motor rehabilitation. In sports training, instead of only showing athletes' actual performance, a more efficient approach for feedback is to simultaneously overlay ideal performance on their actual performance. This manipulation highlights performance errors and has been shown to accelerate athletic training in a variety of sports, such as javelin throw (Hubbard and Alaways 1989), rowing (Fothergill 2010), and sprint (Ilbilge 2014). Also, error feedback with amplified magnitude, as a form of augmented feedback, has been shown to improve the learning of complex motor skills (Hasson et al. 2016; Todorov et al. 1997). Similarly, studies on motor rehabilitation have found that providing augmented error feedback accelerates motor learning in patient populations (Abdollahi et al. 2011; Wei et al. 2005). We would argue that these techniques also enhance error saliency to participants and facilitate their learning. Whether they can enhance retention of acquired skills or recovered motor abilities warrants further investigations.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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AUTHOR CONTRIBUTIONS

W.J. and K.W. conceived and designed research; W.J., X.Y., and C.Y. performed experiments; W.J. analyzed data; W.J. and K.W. interpreted results of experiments; W.J. prepared figures; W.J. drafted manuscript; W.J. and K.W. edited and revised manuscript; W.J. and K.W. approved final version of manuscript.

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