

# Visuomotor adaptation and generalization with repeated and varied training

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**Abstract** Many studies have shown that reaching movements to visual targets can rapidly adapt to altered visual feedback of hand motion (i.e., visuomotor rotation) and generalize to new target directions. This generalization is thought to reflect the acquisition of a neural representation of the novel visuomotor environment that is localized to the particular trained direction. In these studies, participants perform movements to a small number of target locations repeatedly. However, it is unclear whether adaptation and generalization are comparable when target locations are constantly varied and participants reach to visual targets one time only. Here, we compared performance for reaches to a 30° counter-clockwise visuomotor rotation to four targets, spaced 90° apart across four areas of workspace 18 times each (repeated practice (RP)) with one time only reaching movements to 72 targets, spaced 5° apart (varied practice (VP)). For both training groups, participants performed 18 reaches to radial targets (either at the repeated or varied location) in a specific area of the workspace (i.e., one of four quadrants) before reaching in the adjacent workspace. We found that the RP group adapted more completely compared to the VP group. Conversely, the VP group generalized to new target directions more completely when reaching without cursor feedback compared to the RP group. This suggests that RP and VP follow a mainly common pattern of adaptation and generalization represented in the brain, with benefits of faster adaptation with RP and more complete generalization with VP.

**Keywords** Visuomotor adaptation · Generalization · Reaching movements · Motor learning · Visuomotor rotation

## Introduction

Humans can learn to adjust reaching movements to visual targets with altered visual feedback of the hand (i.e., visuomotor rotation) (Krakauer et al. 1999, 2000; Caithness et al. 2004; Bays et al. 2005; Klassen et al. 2005; Wang and Sainburg 2005; Kagerer and Contreras-Vidal 2009) and mechanical perturbations to the arm (i.e., robot-generated pulses or force fields) (Shadmehr and Brashers-Krug 1997; Klassen et al. 2005; Overduin et al. 2006). Typically, when reaching to a single target, the initial cursor deviation is reduced to a saturated level, and participants adapt to a 30° visuomotor rotation of the hand-cursor within 20 trials (Krakauer et al. 2000; Kagerer and Contreras-Vidal 2009). Interestingly, more training trials are required to adapt to a visuomotor rotation when reaching to an increasing number of targets spread across a workspace (Krakauer et al. 2000; Bock 2003). However, it is unclear whether reaching toward many novel target directions one time only within a certain subsection of workspace will lead to a similar adaptation shown previously.

Visuomotor adaptation has been shown to generalize across the workspace, that is, to the untrained directions. Critically, the extent of generalization depends on the parameters of the task. For instance, some studies show significant generalization outside of the trained workspace (Ghilaridi et al. 1995; Imamizu et al. 1995; Vetter et al. 1999), whereas others show limited generalization outside of the trained area (Ghahramani et al. 1996; Pine et al. 1996; Krakauer et al. 2000; Wang and Sainburg 2005; Woolley et al. 2007).

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The discrepancy between these studies may be partly attributed to the nature of the visual distortion; that is, adapting to a shifted or translated hand-cursor discrepancy leads to a broader generalization than adapting to a rotated cursor (i.e., visuomotor rotation) (Cressman and Henriques 2009). Generalization does not appear to be affected by training to one or many different target locations across the workspace when adapting to applied force perturbations of the arm (Mattar and Ostry 2007). Generalization is enhanced when participants adapt reaching movements to multiple target locations across the workspace compared to adaptation of a single target location. However, the extent of generalization declines as the distance between a trained and novel target increases. Specifically, performance significantly declines when reaching to targets radially  $22.5^\circ$  in the clockwise (CW) or counter-clockwise (CCW) direction from a single trained target. Furthermore, there is very limited or no generalization when targets are presented at locations of  $45^\circ$  or further (Krakauer et al. 2000). Likewise, subjects can adapt to opposing rotations to targets that are located at least  $120^\circ$  away with limited interference (Woolley et al. 2007). These results suggest that reach adaptation of a visuomotor rotation is somewhat restricted to a trained direction. Moreover, a recent study proposes a computational neuronal population coding model that may account for the decline in adaptation and generalization when reaching occurs  $22.5^\circ$  away from the previously trained area. This study suggests that the decline in adaptation outside of this particular trained area could be attributed to the width of the tuning curves of neurons in the posterior parietal cortex (Tanaka et al. 2009). In fact, this generalization of the visuomotor rotation may depend on the direction of the movement rather than the final location of the target, even from different start locations (Wang and Sainburg 2005). This suggests that the brain learns visuomotor rotations by remapping the vectors of the movement rather than the final limb positions.

Although the extent and constraints of learning complex visuomotor behaviors and its subsequent use by neural systems to adapt and generalize to different areas of workspace for a small number of target locations repeatedly are known, it is currently unclear whether visuomotor adaptation and generalization are similar when performing reaching movements one time only to different novel targets spaced within a certain section of the workspace. Additionally, it is unclear whether this previously observed adaptation and generalization relates to the number of targets or how far apart these target locations are from each other. Recently, it has not only been shown that the earlier stages of visuomotor adaptation are largely affected by the spacing of the targets across a given workspace, but the later stages are more dependent on the number of trials to each particular target regardless of their spacing across a workspace (Bock and Schmitz 2011). In the current study, participants performed reaching

movements to multiple novel target locations within a close vicinity to distinguish between the effect of proximity and number of target locations on adaptation and generalization. If reaching to multiple novel target locations (varied practice (VP)), even when they are located in the same region, produces a slower rate and less degree of total adaptation than that produced with repeated practice (RP), then this suggests that the brain requires repeated exposure to the same directions to learn the appropriate motor commands. Further, if adaptation is less complete for VP, this may lead to less generalization to novel target directions. Conversely, VP may lead to greater generalization than RP given its increased exposure to a slightly greater span of workspace during training, leading to a broader generalization of reach movements. In this study, two different groups performed reaching movements to a visuomotor rotation while training to a small number of targets repeatedly (RP) or only once to different novel target locations (VP) in a specific area of workspace at a time. Critically, this study investigates the degree of learning of each of these training conditions on adaptation and generalization of the workspace, and consequently on the formation of the appropriate novel motor commands for reaching movements.

## Methods

### Participants

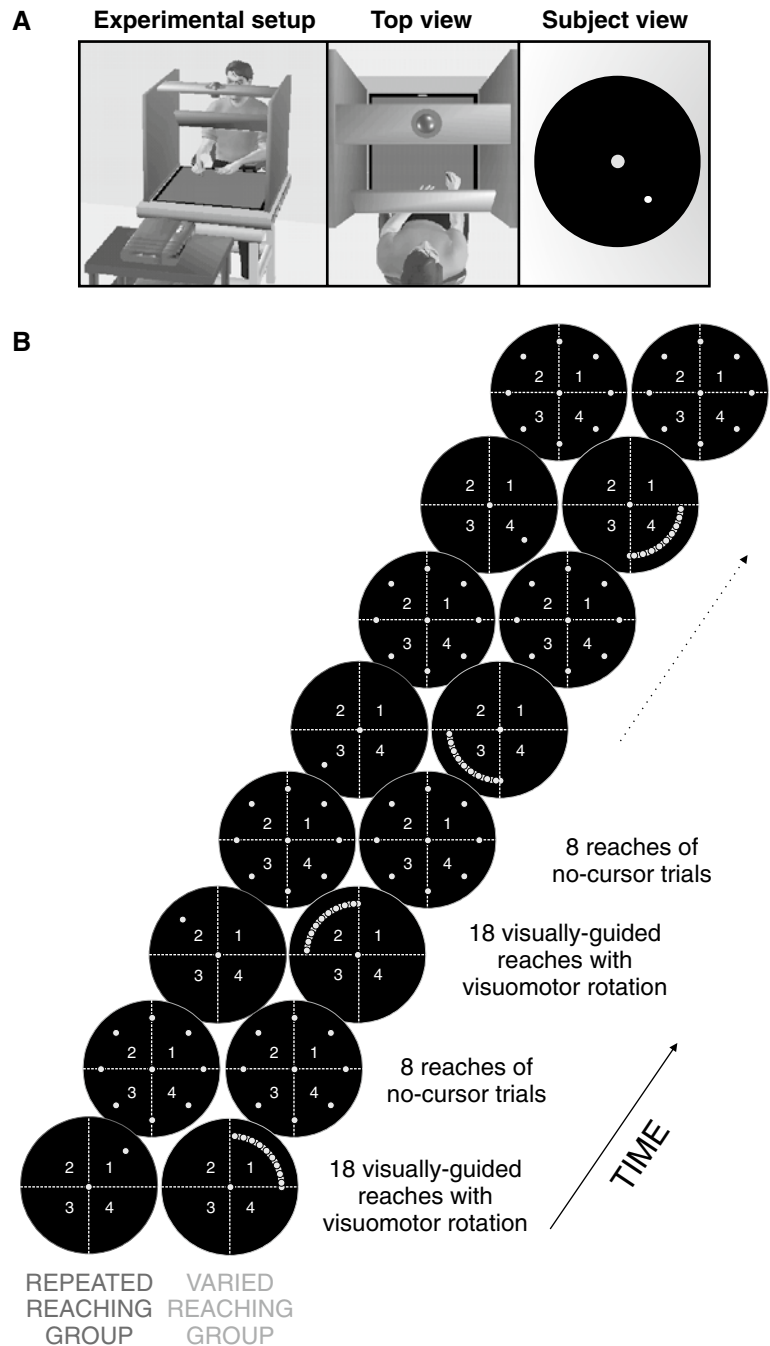
One hundred and sixty participants took part in this experiment (mean age 21 years with standard deviation of  $\pm 5$ ; 103 females). All were naïve to the intent of the experiment and signed a York Human Participants Review Subcommittee approved consent form. Participants received credit in an introductory psychology course for participation. All participants were self-reported right handed, had normal or corrected to normal vision, and had no known neuromuscular deficits.

### Apparatus

Participants sat in a height adjustable chair facing a vertically projected screen placed 65 cm in front of them and moved a hand-held stylus across the surface of a horizontal digitizing tablet with their right arm. Figure 1a shows the experimental apparatus, and the vertical screen is not shown but was within the same plane as the displayed central target. The tablet was positioned 75 cm from the ground, at elbow level, where participants could comfortably move in the horizontal plane. An opaque shield was in place to prevent participants from viewing movement of their hands at all times.

The visual targets and cursor feedback of the unseen hand were viewed in the vertical plane (see Fig. 1a). All

**Fig. 1** Experimental setup and procedure. Participants made reaching movements on a horizontal digitizing tablet (a) while viewing the targets shown (b) and a white circular cursor representing hand position (a–right panel). **b** The training procedure for RP and VP groups. Each group either trained to one target 18 times (RP, rightward panels) or to 18 targets only once (VP, leftward panels) in one area of workspace. Following training to each area participants reached to the 8 radially spaced targets with no-cursor feedback (“no-cursor trials”). The dotted lines in the circles represent the boundaries of each area of workspace, and the numbers indicate an example of the numbered areas (note that these were not visible to participants)



targets were 1.5 cm in diameter, and the cursor was 0.5 cm in diameter. Each target was radially spaced 10 cm from the central target. Cursor position was recorded continuously (Wacom Intuos3, 12" × 12" digitizing surface, resolution of 5,080 lines per inch, sampled every 20 ± 7 ms) (Dionne and Henriques 2008) as participants moved a stylus pen across a digitizing tablet. The movements made by the participants on the digitizing tablet were congruent with the projected image of the cursor in a 1:1 fashion, that is, a movement of 5 cm on the tablet produced a 5-cm movement of the cursor

on the screen. In some trial sets, the cursor moved veridical to the hand, while in other sets of trials, the cursor trajectory was rotated 30° CCW relative to the direction of their hand motion from the home position.

**Procedure**

Participants made out-and-back reaching movements by moving the cursor from a central starting target (Fig. 1) to a peripheral, radial target, pausing briefly at the end of each

movement until the central target reappeared. A successful trial involved a movement from the center to a peripheral target and back to center. Participants were not instructed to look at any particular area of the projection screen, but only to look over the opaque screen of the visual display.

Participants performed three different conditions in either the VP or RP groups: (1) no-cursor control; (2) visuomotor rotation training; and (3) no-cursor trials. The no-cursor trial sets had eight targets, radially spaced  $45^\circ$  apart and 10 cm from the central target, as shown by the target sets in Fig. 1b, labelled at the right with “8 reaches of no-cursor trials”. A control condition was performed once at the beginning of the experiment to provide familiarization and to determine a baseline measure of reaching performance with aligned cursor feedback. Also, one set of no-cursor control trials was performed immediately before training to provide familiarization and baseline reaching performance without visual feedback. Sets of no-cursor trials were then repeated at regular intervals between training sets as illustrated in Fig. 1b, where participants reached once to each of eight radially positioned targets spaced  $45^\circ$  apart. In the no-cursor trials, the cursor was initially visible at the central start position but disappeared as it moved 2 cm away from the center target.

Figure 1b shows the target locations for the visuomotor rotation training conditions for the two groups. In the RP group (leftward panels), participants performed reaching movements repeatedly to one target in each of the four areas of the workspace (a quadrant), while in the VP group (rightward panels), participants performed reaching movements to a novel target location with every trial in each quadrant. For both training groups, the cursor was rotated  $30^\circ$  CCW relative to hand movement. Each of the four training sets involved eighteen reaches with the rotated cursor in one quadrant. This was followed by a set of no-cursor trials to the eight radially positioned targets spaced  $45^\circ$  apart before proceeding to the training trials in the next, adjacent area (Fig. 1b). This was repeated until training was complete in all four quadrants of the workspace with the no-cursor trials following training in each area (Fig. 1b). The spatial location and direction of training in each quadrant were counterbalanced across initial quadrant (1st, 2nd, 3rd or 4th) and the successive quadrant (CW or CCW) for all participants.

In RP, participants performed reaching movements to one target repeatedly per quadrant. In polar coordinates, the target array was  $45^\circ$ ,  $135^\circ$ ,  $225^\circ$ , and  $315^\circ$  (leftward panels in Fig. 1b). In VP, participants performed reaching movements once to eighteen targets, radially spaced  $5^\circ$  apart in each quadrant (rightward panels in Fig. 1b). The first three reaches in each quadrant for VP were to targets located  $40^\circ$ ,  $45^\circ$ , and  $50^\circ$  away from the cardinal axes of the previously trained area, with the remaining targets presented in random order. In this way, the first three targets in each quadrant would be separated by a minimum of  $45^\circ$  from the most

peripheral trained target in the preceding quadrant to assess spatial generalization. Given that generalization decreases substantially for novel targets located  $22.5^\circ$  from the trained target direction (Krakauer et al. 2000), this ensures that at least the first three reaches of both the VP and RP groups for each quadrant should not be influenced by proximity generalization. After training in all four quadrants, participants performed seventy-two reaching movements in total with a rotated cursor in both VP and RP.

#### Data Analysis

The aim of this experiment was (1) to investigate adaptation to a visuomotor rotation when reaching movements are performed to a small number of targets repeatedly (RP) or a novel target every trial (VP) within the same quadrant and (2) to measure generalization across the successive quadrants. All trials were screened with respect to their velocity profile, hand trajectory, rate of movement, and end point position using customized MATLAB software (MATLAB 7.1; MathWorks, Natick MA). For each trial, movement onset and offset were determined to be 10 % of peak velocity. Movement length and/or angular deviation greater than two standard deviations from the mean for training trials were discarded (this accounted for about three percent of all trials). We only analyzed the outward reach from the center to the peripheral targets. Deviation was measured by quantifying the angle at peak velocity. Specifically, angle at peak velocity was calculated by the deviation from a straight line where the velocity of cursor movement was the greatest (Dionne and Henriques 2008; Balitsky Thompson and Henriques 2010). To test our hypotheses, we analyzed two main factors including TRAINING GROUP (RP and VP) and the QUADRANT ORDER of training (1st, 2nd, 3rd, and 4th quadrant), described in detail below.

To measure the extent of adaptation within and across each quadrant for VP and RP, we performed a three-way ( $2 \times 4 \times 2$ ) ANOVA that included TRAINING GROUP, QUADRANT ORDER, and the reach deviations of the initial to final block of three trials (BLOCK) during visuomotor adaptation training. We also performed a two-way ANOVA where the dependent measure was the difference between in the initial and final block (i.e., initial three minus final three trials), as a function of TRAINING GROUP and QUADRANT ORDER. Although analysis was performed on adaptation in each area of workspace, it is possible that adaptation in the first two areas could improve performance in the last two areas, given that rotated cursor feedback was provided on the outward and the return reach. Therefore, the primary interpretation of the analysis performed involved the adaptation in the first two areas of workspace. As a result, we performed two additional ANOVAs with the same factors, but only for the first two QUADRANTS rather than

all four, to avoid the possible confounding variable of return to center feedback during visuomotor adaptation training. To account for multiple comparisons in the four ANOVAs comparing initial and final blocks of reaching errors, we adjusted the alpha-level criteria to  $p = 0.01$  (Bonferroni correction).

We measured generalization in two ways. First, we analyzed the initial three trials of training across each of the four quadrants. We predicted that if the initial deviations were smaller in the adjacent quadrants, then this would suggest generalization across quadrants during training trials. However, if there is no generalization, then this would suggest that quadrants of workspace are learned locally and do not transfer sufficiently to different target directions. We chose blocks of three trials, because we designed the presentation of the targets for the VP group such that the first three trials were approximately along the same diagonal as the single target in the RP group. We compared these initial reaches using a two-way ( $2 \times 4$ ) ANOVA (GROUP \* QUADRANT ORDER). We performed the same two-way ANOVA for the final block of reaches for each training set to assess the amount adaptation across the workspace. Although we included all four quadrants in our analyses, we performed additional ANOVAs which included the same factors, but only for the first and second QUADRANTS. Bonferroni correction method was used to correct for these four ANOVAs at an alpha-level of 0.01.

Our second measure of generalization involved comparing the reach aftereffects (i.e., persistent deviations in reaching after training to a visuomotor rotation) to the eight radial targets without a cursor between the four training sets in their separate quadrants. If generalization occurs, we should see aftereffects for target locations in the untrained quadrants. Given that generalization tends to degrade as novel targets deviate farther from the trained direction, we compared the magnitude of these aftereffects as a function of their relative distance to the single target that represented the trained target for RP or the average trained direction (of the 18 targets) for VP. Here, our main measure was a two-way ( $5 \times 2$ ) ANOVA to compare these reach aftereffects to targets as a function of their distance from the trained direction (five relative locations:  $0^\circ$ ,  $45^\circ$ ,  $90^\circ$ ,  $135^\circ$ , and  $180^\circ$ ) across the two training groups for aftereffects produced after the first training set in the first quadrant. For a final comparison, we also performed the same ANOVA on the aftereffects that followed training in all four quadrants. Bonferroni correction method was used to correct for multiple-comparison post hoc *t*-tests. The alpha-level criteria for the two ANOVAs performed on the aftereffects on reaching after visuomotor adaptation training were adjusted (Bonferroni correction) to  $p = 0.025$ .

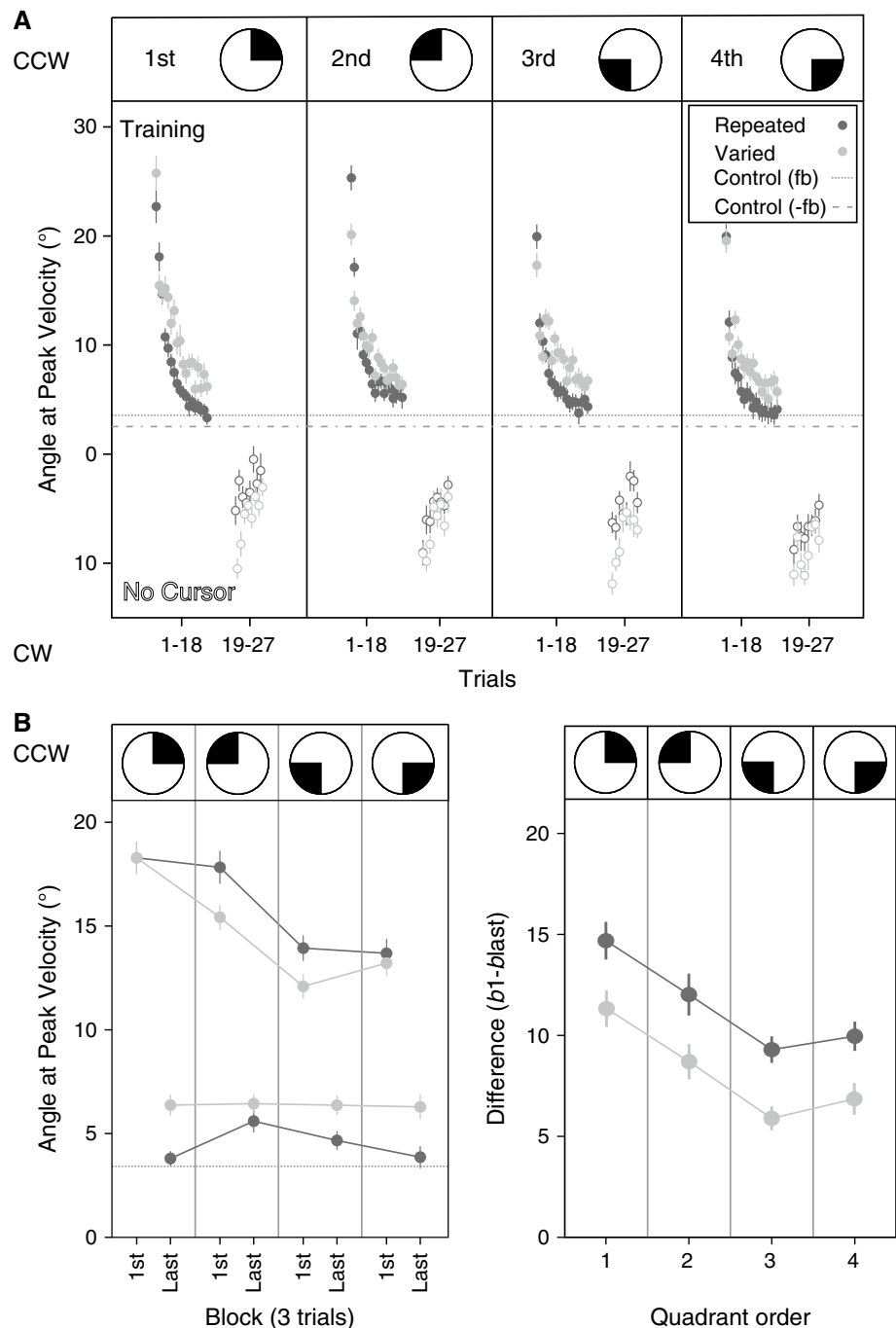
## Results

Figure 2a, b show angle at peak velocity, averaged across all participants, for the training (solid) and the no-cursor trials (unfilled) for the RP (black) and VP (gray) groups. Figure 2a shows reaching deviation across all 18 trials, while Fig. 2b shows the average of the first (circles) and last three (diamonds) training trials (blocks) within each quadrant. The labels (1st, 2nd, 3rd, and 4th) highlight that participants trained in one quadrant and then trained in an adjacent quadrant and does not indicate the spatial location of the quadrant. The horizontal lines represent baseline performance for the two controls (with aligned cursor, dotted, and no-cursor, dashed). During RP (black circles), cursor trajectories follow a typical pattern of adaptation with an initial increase in deviation followed by a decrease over trials within each quadrant. Deviations are similar to baseline performance at the end of the eighteen trials of training in each quadrant. A slightly different pattern of adaptation is observed across training trials for RP and VP groups for the first three quadrants, with consistently greater deviation in the VP group (gray circles), but a similar pattern of adaptation between the two groups for the fourth (last) quadrant. When the extent of the adaptation is quantified by comparing the initial with the last block (Fig 2b), there is a decrease in deviation in all quadrants ( $F(1,414) = 762.04$ ,  $p < 0.0001$ ), with the amount of adaptation differing between groups across successive quadrants ( $F(3,414) = 13.1$ ,  $p < 0.0001$ , interaction) and with greater overall adaptation in the RP than VP group ( $F(1,414) = 34.95$ ,  $p < 0.0001$ ). The same pattern emerges when comparing the initial with the last block across only the first two quadrants.

Figure 2b also shows the patterns of generalization from one area to the next as evident by the significantly decreased deviations for the first blocks (circles) across successive quadrants ( $F(3, 309) = 15.356$ ,  $p < 0.0001$ ). This decrease across quadrants did not vary with the training group (no interaction,  $F(3, 309) = 1.030$ ,  $p = 0.0380$ , Bonferroni corrected alpha 0.01). This suggests that the degree of generalization was somewhat equivalent, although these initial errors were smaller for the VP than for RP, which was nearly significant ( $F(1, 309) = 6.415$ ,  $p = 0.013$ , Bonferroni corrected alpha 0.01). Results were the same after training in the first and second quadrants only. The last block of trials in each area (diamonds in Fig 2b) did not vary with successive quadrants (no interaction,  $F(3, 309) = 0.286$ ,  $p = 0.836$ ) and did not vary among training groups (no interaction,  $F(3,309) = 0.586$ ,  $p = 0.625$ ) although deviations were significantly less and closer to baseline for RP compared to VP ( $F(1, 309) = 15.755$ ,  $p < 0.0001$ ). This is also the case when comparing the last block of trials between the first two quadrants only. Not surprisingly, the amount of adaptation (the difference between the final and initial blocks, as shown



**Fig. 2** Averaged results of adaptation to a visuomotor rotation for the RP (*black*) and VP (*gray*) groups for all participants ( $n = 160$ ) and all trials. The *top* of each panel represents the number order of areas that participants trained. The *circles* with the quarters of shaded areas do not necessarily reflect the actual sequence of locations participants trained, but rather it is a depiction of how participants reached in one area and then moved to the adjacent area (in either the CW or CCW direction). **a** Shows each individual trial (averaged across participants) for training (*solid circles*) and no-cursor trials (*open circles*) for every area. The average of baseline reaching with aligned cursor feedback (*fb*) and baseline reaching for no-cursor control (*-fb*) are shown as the *horizontally dashed lines*. **b** Adaptation and generalization across areas. Each data point represents the average of the first three (*circles*) or last three (*diamonds*) of a particular area of workspace for all participants. Baseline reaching with aligned cursor feedback is shown as the *dotted line*. **c** Each data point is the difference from the first block to the last block in angular error for each area (as shown in **b**). Error bars are SEM

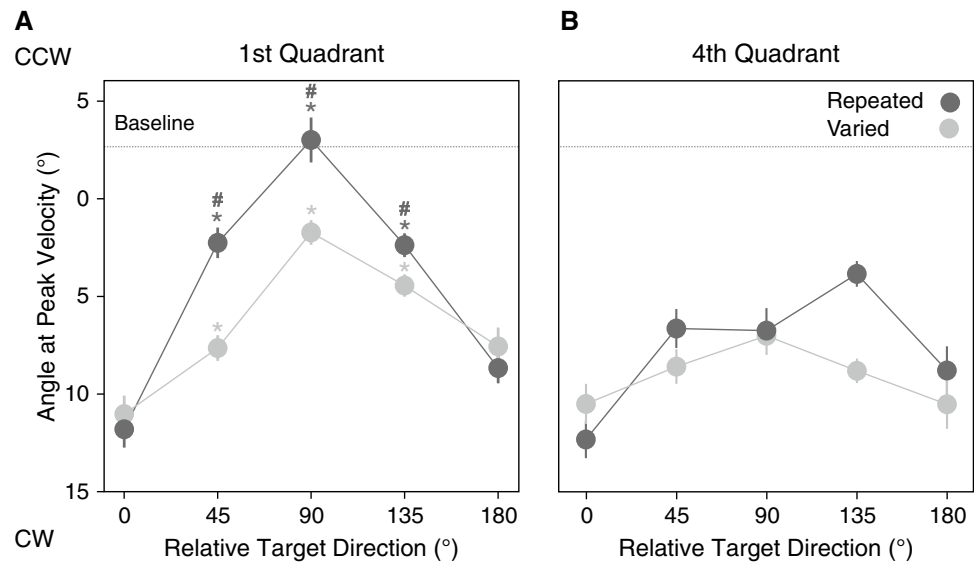


in Fig 2c) was decreased across areas ( $F(3, 471) = 219.534$ ,  $p < 0.0001$ ), mainly due to the lower initial errors for each successive workspace (circles in Fig. 2b) for both groups. This decrease across areas did not vary with training group (no interaction,  $F(3, 471) = .0292$ ,  $p = 0.831$ ), although RP adapted more than VP in that the overall difference between first and last block was larger ( $F(1, 471) = 8.362$ ,  $p = 0.004$ ). This is also the case when comparing between the first two quadrants.

The unfilled circles in Fig. 2a represent reaching deviations with the no-cursor trial sets after training in each quadrant, and these persistent deviations represent aftereffects. Aftereffects, for all eight radial directions, are present for both RP and VP. This is consistent after training in each successive area, suggesting that the degree of adaptation was similar within each quadrant.

Figure 3a shows the averaged results for the no-cursor condition (aftereffects), performed after training in the first

**Fig. 3** Averaged results for the no-cursor trials condition. These aftereffects for each of the target directions shown relative to the previously trained direction (or average direction in the case of VP). Targets in the CW and CCW directions are collapsed. Dashed horizontal line represents baseline reaching in the no-cursor control. Means across all participants and trials are shown with SEM bars. **a** Angle at peak velocity of reaches to the relative targets after training in the 1st area of workspace. **b** Angle at peak velocity of reaches to the relative targets after training on all four areas



quadrant. Each target is plotted by its relative distance from the previously trained direction or quadrant. There was no difference between reaching to targets located either CW or CCW of the trained target ( $p > 0.05$ , Bonferroni corrected); thus, target directions were collapsed in both the CW and CCW directions. Not surprisingly, aftereffects varied as a function of the distance from the trained target ( $F(4, 888) = 37.940$ ,  $p < 0.001$ ), although the pattern of aftereffects was larger for VP (gray symbols,  $F(4, 888) = 3.957$ ,  $p = 0.003$ , group  $\times$  direction interaction). The overall size of the aftereffect was also larger (greater degree of deviation) for VP ( $F(1, 888) = 13.859$ ,  $p < 0.001$ ). Post hoc analysis revealed that RP shows a difference between the previously trained direction ( $0^\circ$  in Fig. 3) and all novel targets ( $p < 0.05$  indicated by black asterisk) except for the  $180^\circ$  target. Similarly, VP shows differences between the average trained direction ( $0^\circ$ ) and all novel targets (significance indicated by gray asterisk) except for the  $180^\circ$  target. When comparing the relative target direction across reaching conditions, post hoc analysis found that aftereffects for VP were greater than RP to all targets except the previously trained target ( $0^\circ$ ) and the  $180^\circ$  target (significance indicated by pound signs in Fig. 3a).

Aftereffects produced after training in all four quadrants were found to be more uniform, as shown in Fig. 3b; although they did differ across the relative directions ( $F(4, 891) = 10.313$ ,  $p < 0.001$ ), the extent of this direction dependency was, not surprisingly, much smaller after training in the first quadrant (compare Fig. 3a, b). The extent that aftereffects varied with relative direction differed between the two groups ( $F(4, 891) = 3.018$ ,  $p = 0.017$ , interaction), with RP showing less overall deviation to the relative targets ( $F(1, 891) = 8.965$ ,  $p = 0.003$ ). Finally, aftereffects did not increase in magnitude for the previously trained target

(Fig. 3a, b,  $0^\circ$  trained target) after training in each successive quadrant for both VP and RP ( $F(3, 619) = 0.087$ ,  $p > 0.05$ ). This suggests that training in one or more quadrants did not lead to accumulative adaptation (or increasingly larger aftereffects) in successive areas.

## Discussion

This study tested how training reaching movements to the same target many times (RP) or to many different but proximate targets only once (VP) affected visuomotor adaptation and generalization to the untrained workspace. The results suggest that RP and VP follow a mainly common pattern of learning and generalization of the workspace with distinct advantages and disadvantages to both types. With RP, the decline in errors and the extent of this decline for each area of workspace is greater, but with less generalization to novel workspace. In contrast, VP results in a slower decrease in errors and final errors that are not reduced to the extent of RP, but with greater generalization to novel workspace. Also, the results demonstrate that some generalization can occur to a certain extent to targets up to  $90^\circ$  away during training to a visuomotor rotation and after training when reaching with no-cursor feedback.

Many of the current results are consistent with and extend previous research, which suggests adapting to a visuomotor rotation is local to particular trained locations (Krakauer et al. 2000; Wang and Sainburg 2005). In each area of workspace, during RP and VP, initial errors and the decrease in errors across trials are fairly similar. In addition to previous findings, there was a small amount of generalization for targets located on average up to  $90^\circ$  apart with both visuomotor training groups, even after a brief bout of training,

that is, 18 or 36 trials. A small amount of generalization to targets 90° away has been shown by other research (Wang and Sainburg 2005), while others show no generalization to untrained targets at such a distance (Krakauer et al 2000). Although we also found perfect generalization to novel targets 180° away relative to the trained location after training in one quadrant, in contrast to previous findings (Krakauer et al. 2000; Woolley et al. 2007), this is likely due to the fact that rotated cursor feedback was given on the return reach to center, and this is quite similar to the outward reach to the target 180° away.

#### Visuomotor adaptation with repeated versus varied reaching

One of the main goals of this work was to investigate how visuomotor adaptation is affected by training with many different target locations only once. It has been demonstrated that only 20 to 60 trials are needed for adaptation to a point where significant decreases in deviation are no longer observed (saturation) (Krakauer et al. 2000). It takes fewer trials to adapt to saturation when reaching to one target (closer to 20 trials) compared to reaching to two, four, and eight targets spread across a workspace. Specifically, training with eight different targets spread across a workspace produces a slower rate of adaptation and to a lesser extent than training repeatedly to a single target with the same number of total reaches. In the current study, there was slightly less adaptation when reaching to eighteen various targets in near proximity compared to adaptation of only one target, although the discrepancy was not as large given that the various target locations fell within the same area (90° of workspace). A recent study showed that increasing the number of target locations even within a close proximity (from 2 to 8 targets within 42°) slowed the adaptation rate (Bock and Schmitz 2011). This indicates that similar to our study, the number of targets affects the degree of adaptation, regardless of the spread across a workspace. However, the current study further extends this research by ensuring that participants in VP were reaching to novel locations with every trial. The current study further explores the novel question of whether multiple repetitions to similar targets are required or especially conducive for visuomotor adaptation and whether a similar pattern of adaptation could be achieved with no opportunity to repeat reaches to any target location. Further analysis on the extent of adaptation within and across areas of workspace revealed that RP and VP followed a similar pattern of adaptation in each area, although RP always showed greater levels of adaptation. If the brain adapts to a visuomotor rotation differently with both types of training, there would be a different pattern of adaptation within and across areas of workspace. This indicates that although RP produces more complete adaptation within

each area of workspace, the brain can similarly use information from multiple novel target directions (VP) to deduce the proper motor commands necessary to correct reaching movements for a visuomotor rotation.

#### Generalization of the workspace

Visuomotor adaptation has been shown to be localized to particular directions, and there is moderate generalization and considerable decay outside of the trained area (Ghahramani et al. 1996; Pine et al. 1996; Krakauer et al. 2000; Wang and Sainburg 2005; Woolley et al. 2007). Participants generalize visuomotor adaptation across different target distances and arm configurations after training to a single target. However, after training in a single direction, there is very little generalization to other directions, especially those 45–90° from the trained target location. There is perfect generalization to untrained directions only when participants train to all eight equally spaced targets such that the novel targets were located only 22.5° from any of the trained targets. Therefore, it seems that the brain acquires a localized visuomotor adaptation rather than developing a global generalization of the workspace after training to one particular direction (Krakauer et al. 2000). Furthermore, visuomotor adaptation has been shown to be localized to the trained movement vector/direction, as there is 100 % generalization to targets that are similar in direction and extent to those previously trained. There was less generalization to targets with different movement vectors, even when some of these final target locations remain the same (Wang and Sainburg 2005). Moreover, difficulties in adapting to two opposing visuomotor rotations within the same training session suggest that visuomotor adaptation is localized to a trained region. Participants could adapt to two opposing rotations only when there was a radial separation in workspace of 180°, suggesting that adaptation of a visuomotor rotation is localized to the trained area (Woolley et al. 2007).

In these studies, participants were familiarized to local areas of the workspace by reaching to a small number of target locations repeatedly. The current study investigated the idea that having a more widespread and non-repetitive sample of the workspace might lead to differences in generalization. There was slightly more generalization with RP and VP than perhaps expected. Generalization has been found to target directions up to 90° radially spaced from the trained direction, even when the trained and novel targets were within different areas of the workspace (Wang and Sainburg 2005). This finding is consistent with the current finding of a small but significant amount of generalization to targets that are separated up to 90° for RP and 90° (on average) separated for VP, when reaching with rotated cursor feedback. Also, this study extends previous research by demonstrating that this generalization occurs similarly when training



with all novel targets within a subset of workspace. It is important to note that this generalization occurred with very few training trials (18 trials within each area) for both training groups. Overall, the current study found slightly more global generalization to targets outside of the trained workspace similar to other studies (Imamizu et al. 1995; Vetter et al. 1999; Ghez et al. 2007). While the extent of adaptation that arose with varied reaching with a rotated cursor may have been suboptimal, it may have been more applicable to a larger sample of movement directions and thus allows for slightly more generalization.

Assessing aftereffects was another way, we further investigated how having a more widespread and non-repetitive sample of the workspace might lead to differences in generalization, compared to the traditional repetitive training protocols. The current study is the first to demonstrate that generalization across a large portion of the radial workspace is slightly enhanced when reaching to all novel targets in one proximal subsection of workspace. This is demonstrated more clearly by the pattern of aftereffects for both reaching groups, with VP leading to a slightly greater generalization of the workspace compared to RP when reaching without cursor feedback. Therefore, it seems that a broader sample of a subsection of workspace leads to a more global generalization of a wider directional spread, as other studies have suggested (Imamizu et al. 1995; Vetter et al. 1999; Ghez et al. 2007) and the current study has demonstrated.

## Conclusion

People are able to adapt to a visuomotor rotation when reaching to a novel target every trial compared to typical visuomotor training of a small number of target directions repeatedly. These two types of training are partially distinct when adapting reaching movements to one area of workspace at a time. RP leads to greater adaptation than VP, whereas VP generalizes to the untrained workspace more broadly than RP does (up to 90° for VP). It, therefore, seems that if the brain has a broader sample of the workspace, it is able to generalize the newly adapted visuomotor movements to untrained areas, but with a detriment to early adaptation.

As shown before, the newly adapted visuomotor movements are likely formed based specifically on the trained target directions. Additionally, the current results suggest that the brain forms the appropriate motor adjustments for a visuomotor rotation differently depending on training repeatedly to one familiar target compared to many different targets only once. The current study suggests one type of training is more beneficial than the other depending on whether greater and more specific adaptation or a broader generalization is the desired goal. It seems that the brain

can more completely deduce the proper motor adjustments required in learning a complex skill when repeating the same movements many times, thus resulting in a detriment to applying this skill in new environments. Conversely, perhaps learning of a specific skill is less complete, but this learning is generalized better when the practiced movements are more random and varied.

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