

# Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace

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**Abstract** Studies have shown that adapting one's reaches in one location in the workspace can generalize to other novel locations. Generalization of this visuomotor adaptation is influenced by the location of novel targets relative to the trained location such that reaches made to novel targets that are located far from the trained target direction (i.e.,  $\sim 22.5^\circ$ ; Krakauer et al. in *J Neurosci* 20:8916–8924, 2000) show very little generalization compared to those that are closer to the trained direction. However, generalization is much broader when reaching to novel targets in the same direction but at different distances from the trained target. In this study, we investigated whether changes in hand proprioception (proprioceptive recalibration), like reach adaptation, generalize to different distances of the workspace. Subjects adapted their reaches with a rotated cursor to two target locations at a distance of 13 cm from the home position. We then compared changes in open-loop reaches and felt hand position at these trained locations to novel targets located in the same direction as the trained targets but

either at a closer (10 cm) or at a farther distance (15 cm) from the home position. We found reach adaptation generalized to novel closer and farther targets to the same extent as observed at the trained target distance. In contrast, while changes in felt hand position were significant across the two novel distances, this recalibration was smaller for the novel-far locations compared to the trained location. Given that reach adaptation completely generalized across the novel distances but proprioceptive recalibration generalized to a lesser extent for farther distances, we suggest that proprioceptive recalibration may arise independently of motor adaptation and vice versa.

**Keywords** Visuomotor adaptation · Hand proprioception · Generalization · Motor learning · Reaching · Sensory plasticity

## Introduction

When reaching to a target, the central nervous system (CNS) depends on sensory information provided by vision (i.e., the sight of the hand, the target and/or the workspace) and proprioception (i.e., limb position) to compute the required motor commands. A mismatch between visual and proprioceptive estimates of limb position has been shown to lead to realignment or recalibration of these conflicting sensory inputs (which is known as sensory remapping or proprioceptive recalibration) in order to create a unified estimate of limb location. Currently, it is unclear how proprioceptive recalibration is related to sensorimotor adaptation.

To study proprioceptive recalibration and sensorimotor adaptation, one can have subjects reach in a virtual reality environment with distorted visual feedback of the hand.

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For example, visuomotor adaptation is commonly studied by having subjects reach to visual targets, while their hand location is visually misrepresented by a cursor on a screen (Ghilardi et al. 1995; Wolpert et al. 1995; Ghahramani et al. 1996; Krakauer et al. 1999; Abeele and Bock 2001; Cressman and Henriques 2009). When subjects first train to reach to a target(s) with distorted visual feedback of the hand (e.g., a cursor that is rotated or translated relative to the hand's actual movement), the cursor appears to initially deviate from the target. Movements are then adjusted or adapted gradually across trials so that later reaches bring the cursor more directly to the target(s) (Ghahramani et al. 1996; Krakauer et al. 1999; Vetter et al. 1999; Baraduc and Wolpert 2002; Wang and Sainburg 2005). In addition to seeing changes in reaches when visual feedback is present, subjects continue to exhibit deviated reaches when the cursor is removed (these deviations are known as aftereffects).

From visuomotor adaptation studies, it is evident that learning or adapting to reach in one location in the workspace can transfer or generalize to other novel locations across the workspace (Ghilardi et al. 1995; Imamizu et al. 1995; Ghahramani et al. 1996; Krakauer et al. 2000; Poggio and Bizzi 2004; Pearson et al. 2010). Generalization of visuomotor adaptation has shown to be influenced by the type of distortion introduced (i.e., cursor gain or cursor rotation) and the coordinates of the targets in the workspace (i.e., target distances and directions relative to the start position and trained target). Reach adaptation to a cursor rotation to a single target leads to a local or narrow generalization pattern across novel-untrained directions such that generalization is only seen at targets near the training target(s) (Krakauer et al. 2000; Wang and Sainburg 2005; Pearson et al. 2010; Neva and Henriques 2013). Increasing the number of trained directions leads to the same local pattern of generalization occurring for each trained direction, resulting in greater overall generalization across the workspace.

In addition to examining generalization of reach adaptation across movement directions, Krakauer et al. (2000) tested how reach adaptation generalized to targets at different distances. They found that after subjects adapted their reaches to a single target (7.2 cm from the start position) with a cursor that was rotated 30° relative to hand movement, subjects successfully adapted their reaches to a similar extent to novel targets in the same direction but at different distances from the start position (2.4, 4.8, and 9.6 cm). In another study by Shabbott and Sainburg (2010), subjects adapted their reaching movements to eight targets located 15 cm away from the home position after training with a 30° CW cursor rotation. Results indicated that subjects completely generalized their adapted reaches to novel targets located 22.5 cm away from the home position (in the same directions as the trained targets). These findings indicate

that generalization of reach adaptation is influenced by the directions and distances of the novel/untrained targets.

In addition to reach adaptation, changes in felt hand position arise after training with distorted visual feedback of the hand (Henriques and Cressman 2012). Changes in felt hand position (or proprioceptive recalibration) have been studied in our laboratory by having subjects estimate their hand position relative to a reference marker in a task that does not require them to reach to a target. Thus, this task eliminates any potential motor confounds. Our results consistently show that subjects recalibrate their sense of felt hand position following reach adaptation to a visual distortion such that they begin to feel their hand is shifted in the direction of the visual feedback provided. Furthermore, other studies using a velocity-dependent force-field perturbation have shown that after subjects adapt their reaches to the perturbation, their perceived sense of hand movement is also shifted (Ostry et al. 2010; Mattar et al. 2013).

Although reaching with distorted visual feedback of the hand leads to changes in the felt hand position and reach adaptation, it has been suggested that these changes may be driven by different error signals. In support of this independence, it has been shown that intact arm proprioception is not necessary for adapting to misaligned visual feedback of the hand. Specifically, it has been shown that when proprioceptive feedback is degraded by agonist–antagonist muscle vibration (Pipereit et al. 2006; Bock and Thomas 2011) or not existent in the case of deafferented patients (Ingram et al. 2000; Bernier et al. 2006), subjects still adapt their movements in response to a visual distortion.

In accordance with these findings, Cressman and Henriques (in revision) have shown that the generalization patterns of proprioceptive recalibration and reach adaptation are different. Specifically, Cressman and Henriques (in revision) showed that independent of reach adaptation (which showed a similar localized generalization pattern as seen in Krakauer et al. 2000; Wang and Sainburg 2005), proprioceptive recalibration generalized across novel locations, in particular targets in novel directions. Recently, Izawa et al. (2012) also examined sensory and motor generalization. In their task, they looked to determine perceived movement direction of the unseen hand following reach adaptation (rotated cursor) to a single target. Izawa et al. (2012) found changes in perceived movement direction of the hand (following visuomotor adaptation) and that the size of this change varied with the direction of movement relative to the trained direction. Importantly, the pattern of these changes in felt (or what the authors called predicted) hand motion differed a bit from the pattern of reach aftereffects across the same range of novel movement directions. Taken together, these findings suggest that motor and sensory changes may be two independent processes arising after training with distorted visual feedback of the hand.

In order to investigate the relationship between reach adaptation and proprioceptive recalibration in more detail, we examined whether proprioceptive recalibration followed the same generalization pattern as reach adaptation when assessed at targets at different distances across the workspace. Specifically, we trained subjects to reach to two visual targets with rotated visual feedback of the hand (i.e., 45° CW rotated cursor) and then we assessed the generalization patterns of both reach adaptation and proprioceptive recalibration to novel locations at different distances relative to the hand start position.

## Methods

### Subjects

In total, 13 right-handed subjects (mean age = 22, SD = 2.34, seven males and six females) participated in this study. All subjects had normal or corrected-to-normal vision. Subjects were pre-screened verbally for self-reported handedness and any history of visual, neurological, and/or motor dysfunction. All subjects provided informed consent in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee and received credit toward an undergraduate psychology course.

### General experimental setup

The experimental setup is illustrated in Fig. 1a. Subjects were seated in a height adjustable chair to ensure that they could easily see all of the targets presented on a reflected screen

and comfortably reach to all target locations. Subjects were asked to hold on to the vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA) with their right hand, so that their thumb rested on top of the handle. The reflective screen was mounted horizontally 8.5 cm above the robot manipulandum. A monitor (Samsung 510 N, refresh rate 72 Hz) located 17 cm above the robotic handle projected visual stimuli such that images displayed on the monitor appeared to lie in the same horizontal plane as the robotic handle. The room lights were dimmed, and the subjects' view of their hand was blocked by the reflective screen as well as a dark cloth draped between the experimental setup and subjects' shoulders.

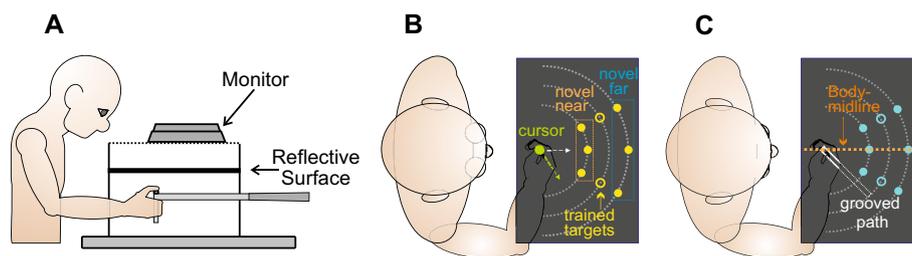
### Procedure

Similar to our previous studies (e.g., Mostafa et al. 2014), the experiment consisted of two separate testing sessions completed on separate days. Each testing session involved four tasks. On the first testing day, the hand cursor for the reach training trials was aligned with the hand (for baseline measures) while on the second testing day, the cursor was rotated 45° clockwise (CW) relative to the actual hand position with the origin of the rotation at the starting hand position. The descriptions and order of tasks completed are outlined below and in Fig. 2.

#### First testing session tasks

##### Aligned reach training task

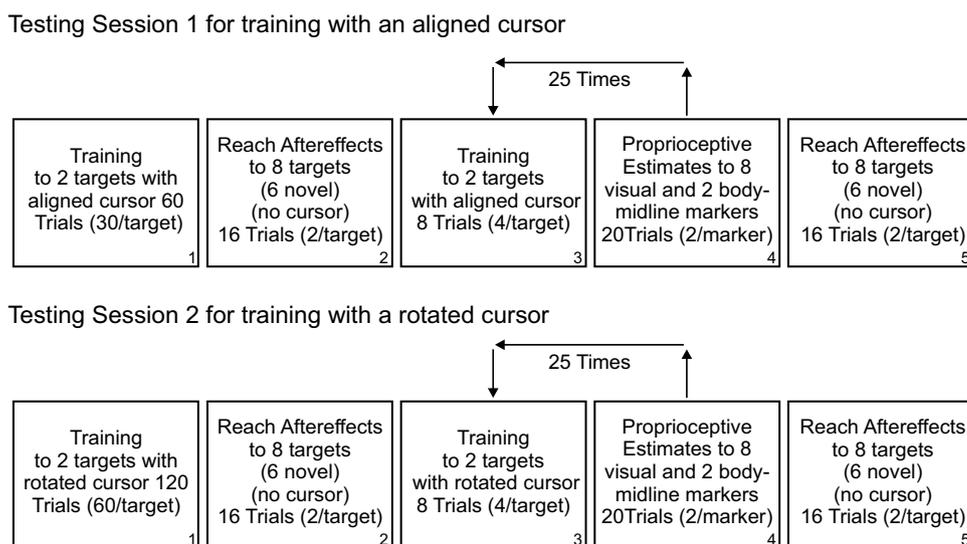
The first testing session included aligned reach training trials (boxes 1 and 3 in Fig. 2), where subjects were asked to



**Fig. 1** Experimental setup and design. **a** Side view of the experimental setup. **b, c** Top view of experimental surface visible to subjects. The home position was located approximately 20 cm directly in front of subjects' midline and is represented by a hand cursor (1-cm-diameter green disk) in **(b)**. **b** Display for reaching tasks. Dotted white arrow shows the cursor path in the aligned training task (aligned with hand path); dotted green arrow shows the cursor path in the misaligned training task (rotated 45° rightward relative to hand path). Training targets were located along a circular arc, 13 cm from the home position at angles of 30° CW and CCW relative to body midline and are shown by the yellow hollow disks. Novel (generalization) reach targets used for the no-cursor reaching task were positioned 0°

and 30° on either side of center, 10 cm (novel-near set; orange edged rectangle) and 15 cm (novel-far set; blue edged rectangle) away from the home position and are shown by yellow solid disks. **c** Location of visual and proprioceptive reference markers for the proprioceptive estimation task; two were located in the same positions as the reach training targets (blue hollow disks), three at novel-near locations, and three at novel-far locations (blue disks). Non-visual reference markers, indicated by the dotted orange line in line with subjects' midline, were at distances of 10 cm or 15 cm from the home position. The white dotted rectangle shows an example of the robot grooved path (color figure online)

**Fig. 2** Schematic showing the order in which the tasks were completed within a testing session. Both testing sessions followed the same order of tasks. The difference between the sessions was the visual feedback provided in the reach training tasks. The cursor was either aligned with the hand (*session 1*) or rotated 45° clockwise (CW) relative to the hand (*session 2*)



reach (as quickly and accurately as possible) to a visual yellow target disk (1 cm in diameter, Fig. 1b) with their right hand hidden from view, but represented by a cursor (green disk, 1 cm in diameter, Fig. 1b) located directly above their thumb. In front of the home position, which was located approximately 20 cm in front of subjects, there were two reach targets located radially 13 cm from the home position at 30° left (CCW) and 30° right (CW) of center (Fig. 1b). The reach trial was considered complete when the center of the cursor had moved to within .5 cm of the target's center. At that point, both the target and cursor disappeared and the robot was locked to a grooved path. This grooved path guided subjects back to the home position by a direct linear route in the absence of visual feedback. If subjects attempted to move outside of the established path, a resistance force [proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s)] was generated perpendicular to the grooved wall (Henriques and Soechting 2003). In this task, there were 60 reach training trials, 30 trials for each target.

#### *No-cursor reaching task*

Immediately after the aligned reach training task, subjects reached to the same two targets plus six novel targets two times each without a cursor (no-cursor reach trials, boxes 2 and 5 in Fig. 2). The six novel targets were located radially along two arcs 10 or 15 cm (i.e., near and far with respect to the hand home position) at 30° left (CCW), 30° right (CW), and 0° in front of the home position (yellow disks, Fig. 1b). In this task, a trial started with the robot handle at the home position and, after 500 ms, the home position disappeared and one of the eight reach targets appeared. Subjects were asked to reach to the visible target (as in the

previous task) with the robot handle but this time without the cursor or any visual feedback of their hand. Once the no-cursor reach movement was complete (final position was held for 250 ms), the target and the home position disappeared, cuing subjects to move back to the home position along a constrained path to begin the next trial. This task was repeated again after the proprioceptive estimate task described below.

#### *Proprioceptive estimates task*

A proprioceptive estimate trial (boxes 4 in Fig. 2) began with subjects grasping the robot manipulandum that was positioned at the home position. Subjects were then asked to actively push the robot handle outwards along a constrained path to a location somewhere along the dotted lines shown in Fig. 1c (dotted lines are for illustration purposes only and were not visible to the subjects). Once the hand arrived at its final position, one of the eight visual reference markers (two are the trained locations and six novel locations) appeared or subjects would hear a beep (which indicated that they were to use their body midline as a reference marker). At this point, subjects were to indicate whether their hand was to the right or left of the reference marker (using the right or left arrow keys on a keyboard). The 10 reference markers for the proprioceptive estimates were located radially along three arcs 10, 13, or 15 cm (i.e., near, trained, and far, respectively, relative to the hand home position), in front of the home position (blue disks, Fig. 1c). Two of the 10 reference markers were located 10 and 15 cm at 0° directly in front of the home position and were represented proprioceptively. These proprioceptive reference markers positions were based on an internal representation of body midline.

The position of the hand with respect to each reference marker was adjusted over trials using an adaptive staircase algorithm (Treutwein 1995). For each reference marker, there were two corresponding staircases, a left and a right, that were adjusted independently and randomly interleaved across 50 trials for each marker. Each staircase began such that the hand was 20° to the left or right of the reference marker. The position of the hand was then adjusted over trials depending on a subject's pattern of responses such that the differences between hand locations in subsequent trials (step size) decreased each time subjects reversed their response pattern from left to right or from right to left within a particular staircase. This ensured that subjects were tested more frequently at positions closer to their sensitivity threshold. If subjects responded consistently, the two staircases converged toward a certain position at which subjects had an equal probability of reporting left or right. This position represented the location at which subjects perceived their hand was aligned with the reference marker.

The proprioceptive estimates trials were systematically interleaved with reach training trials (boxes 3 and 4 in Fig. 2). Subjects began by completing an additional eight reach training trials with a cursor to the reach training targets located 13 cm at 30° right or left of center from the home position. These reaches were then immediately followed by a set of 20 proprioceptive estimate trials. The test sequence of eight reach training trials followed by 20 proprioceptive estimates was completed 25 times in order that 50 proprioceptive estimates were made for each reference marker. There were 700 trials in this task: 200 reach training trials in total, 100 trials per target, and 500 proprioceptive estimate trials in total, 50 trials for each reference marker.

#### Second testing session tasks

The tasks for the second testing session were similar to the first except for the reach training task which involved a misaligned cursor (box 1 in testing session 2, Fig. 2). In this misaligned reach training task, the cursor was gradually rotated 45° rightward (CW, .75° per trial) with respect to the actual hand position. Subjects completed 120 trials in this task. This task was then followed by the no-cursor reaching task and the proprioceptive estimate task (which included reach training trials with the rotated cursor), followed by a final no-cursor reaching task.

#### Data analysis

##### *Reach adaptation*

Directional deviations of the hand made during reaching trials without visual feedback of the hand (no-cursor trials,

open-loop reaches) were analyzed to assess reach adaptation. Reach endpoint errors were defined as the angular difference between a movement vector (from the home position to reach endpoint) and a reference vector (from the home position to the target). Reach errors at peak velocity were defined as the angular difference between a movement vector joining the home position and the position of the hand at peak velocity and the reference vector. The difference between these errors following rotated-cursor training compared to aligned-cursor training, which we will refer to as reach aftereffects (i.e., baseline reaching errors subtracted from reaching errors following training with a rotated cursor), was analyzed to determine whether subjects adapted and generalized their reaches to the trained and novel targets after aiming with a rotated cursor. Subjects completed the no-cursor reaching trials right after the initial reach training and again after the proprioceptive estimate task, so that we could determine whether the extent of reach adaptation remained similar across the testing session. We analyzed mean reach endpoint errors and reach errors at peak velocity in the no-cursor reaches in a two visual feedback condition during the reach training task (i.e., aligned vs. rotated cursor)  $\times$  2 Epoch (trials completed before vs. after the proprioceptive estimate task)  $\times$  3 Workspace (trained vs. novel-near vs. novel-far) repeated measures analyses of variance (RM-ANOVA). We used workspace (or distance) as a factor for both reach aftereffects and proprioceptive bias (described below) rather than target/marker locations because (1) our previous studies showed no systematic differences between direction of trained targets/markers across a similar range of directions and (2) to reduce the number of levels of comparisons (two trained sites vs. six or eight novel sites) to the main ones of interest (distance, or workspace). To test whether the size of possible aftereffects varied as a function of workspace, any significant interaction between visual feedback condition and workspace was followed up by a one-tailed pairwise *t* test comparing the difference in aftereffects across the trained workspace and each of the two novel workspaces (near and far).

##### *Proprioceptive estimates of hand position*

A logistic function was fitted to each subject's responses for each reference marker in each testing session in order to determine the location at which subjects perceived their hand to be aligned with a reference marker. From this logistic function, we calculated the bias (the point at which the probability of responding left was 50 %). This bias value is a measure of subjects' accuracy of proprioceptive sense of hand position (Cressman and Henriques 2009).

Proprioceptive recalibration was assessed by comparing the proprioceptive biases or estimates of hand position

after training with a rotated cursor with those following an aligned cursor (baseline). To do this, we ran a two-way RM-ANOVA with visual feedback (aligned- vs. rotated-cursor training) and workspace (trained vs. novel-near vs. novel-far). Additionally, to test whether the size of possible changes in bias varied as a function of workspace, any significant interaction between visual feedback training condition and workspace was followed up by one-tailed pairwise *t* test to compare the difference in biases across the trained workspace and each of the two novel workspaces (near and far).

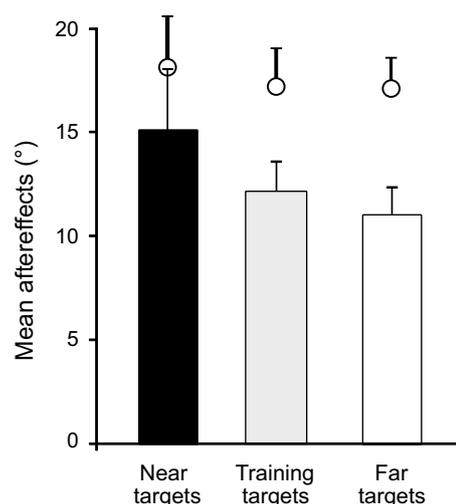
All ANOVA results are reported with Greenhouse–Geisser corrected *p* values. Differences with a probability of  $<0.05$  were considered to be significant. The post hoc tests were Bonferroni corrected to determine the locus of these differences ( $\alpha = 0.05$ ).

## Results

### Reach adaptation generalizes to different target distances

We examined whether subjects adapted their reaches to the visual distortion by assessing their reach errors when reaching without visual feedback (no-cursor reach trials). In Fig. 3, we depict mean no-cursor reaching endpoint errors (aftereffects) relative to baseline performance (i.e., errors achieved after training with an aligned cursor subtracted from errors achieved after training with a rotated cursor). Overall, we found a significant shift in subjects' no-cursor reaches following rotated-cursor training compared to aligned-cursor training ( $F(1,12) = 50.947$ ;  $p < .001$ ), and this shift was opposite to the direction of the introduced distortion. Thus, subjects adapted their reaches in response to training with the rotated cursor. Additionally, the size of reach aftereffects did not differ significantly between reaches completed following reach training trials compared with reaches completed following the proprioceptive estimate trials ( $F(1,12) = .139$ ;  $p = .716$ ). This suggests that the level of reach adaptation was maintained across the testing session.

More interestingly, we found that the extent of reach adaptation for the trained targets [ $12.2^\circ$ , Fig. 3, middle gray bar] and for the novel targets [ $15.1^\circ$  and  $11^\circ$  for near and far targets, respectively], Fig. 3, black and white bars] did not differ significantly ( $F(2,24) = 2.993$ ;  $p = .10$ ; i.e., there was no significant interaction between visual feedback training condition and workspace). This suggests that reach adaptation generalized to a similar extent to all novel targets located at different distances from the trained targets. Analysis of reaching errors at peak velocity (circles in Fig. 3) also revealed significant reach adaptation ( $F(1,12) = 75.002$ ;  $p < .001$ ) and a similar pattern of

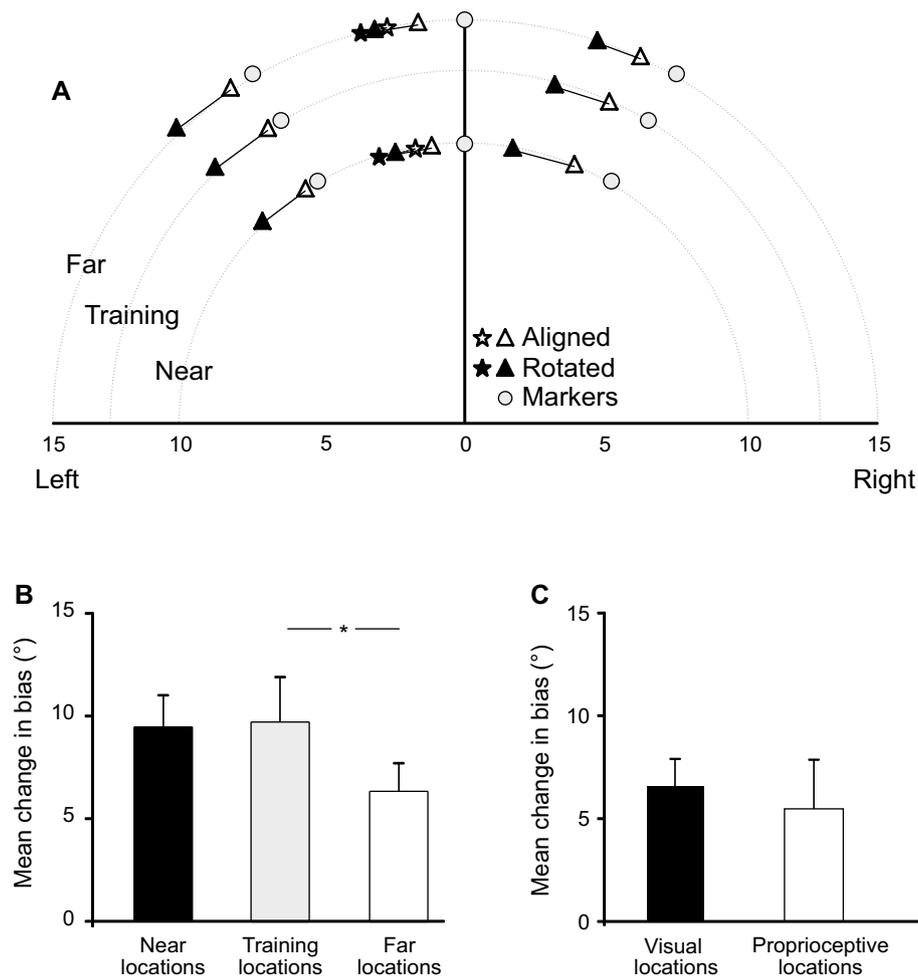


**Fig. 3** Reach aftereffects: difference in mean angular reach endpoint error for the no-cursor reaches after training with misaligned visual feedback for training targets, novel-near targets, and novel-far targets relative to baseline performance. Circles represent mean changes in reaching errors at peak velocity. Error bars reflect the standard error of the mean (SEM)

generalization across novel target locations, in that change in angle at peak velocity did not differ between trained and novel targets ( $F(2,24) = .325$ ;  $p = .622$ ).

### Proprioceptive recalibration generalizes to a lesser extent at far distances

Figure 4a depicts a two-dimensional view of the positions at which subjects perceived their hands to be aligned with the reference markers (gray circles) after training with an aligned (empty symbols) and rotated cursor (filled symbols). These results show that subjects' estimates of their felt hand position after training with a rotated cursor were significantly shifted by  $8.5^\circ$  compared to their estimates after training with aligned cursor ( $F(1,12) = 27.077$ ;  $p < .001$ ). This suggests that subjects recalibrated their perceived hand position after training with the rotated cursor in the same direction as the introduced visual distortion. However, this significant change in bias varied as a function of workspace ( $F(2,24) = 4.797$ ;  $p = .029$ ) in that changes in bias at the trained target locations were  $9.6^\circ$ , while the change was  $9.4^\circ$  and  $6.3^\circ$  at the novel-near and novel-far reference markers locations, respectively (Fig. 4b). When we explored this interaction, we found that these changes in bias were significant at each of three workspaces ( $p < .001$ , Bonferroni corrected). Moreover, additional one-tailed pairwise *t* tests showed that this change was modestly but significantly smaller for novel-far compared to trained positions ( $p = 0.03$ ) but not when comparing novel-near to trained positions ( $p = .855$ ). To



**Fig. 4** Proprioceptive biases following training with aligned and rotated visual feedback of the hand. **a** Mean 2D biases in the proprioceptive estimate tasks relative to the reference marker locations (*gray disks*) after training with aligned visual feedback (*unfilled symbols*) and after training with misaligned visual feedback (*filled symbols*). *Triangles* are those estimates when the reference marker was visual, while *stars* are those estimates made relative to the body midline (proprioceptive reference markers). The *horizontal axis* represents the distance from the home position in centimeters, and the *vertical axis* is in line with the subject's body midline. *Circular arcs* represent different distances in the workspace based on their distance

rule out whether the smaller changes for novel-far locations may be due to only one or two of these locations, we compared whether these proprioceptive changes varied significantly across the four novel-far markers and we found they did not ( $F(3,36) = 1.506$ ;  $p = .243$ ). Moreover, when we compared the proprioceptive (center) reference markers with the novel visual (center) reference markers (see Fig. 4c), to ensure that these results were not due to the modality of the center reference markers, we found no significant differences in changes in felt hand position after training with an aligned cursor compared to rotated cursor for the two marker modalities ( $F(1,12) = .211$ ;  $p = .654$ ).

from the home position; 10 cm (novel-near workspace), 13 cm (training location), and 15 cm (novel-far workspace). **b** Mean changes in bias after visuomotor adaptation relative to those following aligned-cursor training for reference markers at different distances from the home position (training location indicated by the *gray bar*, novel-near shown with a *black bar*, novel-far shown with a *white bar*) and **c** mean change in bias for different reference marker modalities (the *black bar* represents estimates relative to visual reference markers, and the *white bar* represents estimates relative to proprioceptive reference markers). *Error bars* represent the SEM

These results suggest that proprioceptive recalibration generalized to the novel reference markers locations, but to a lesser extent to markers at far distances where participants did not experience the altered visual feedback of the hand.

## Discussion

Our goal was to determine whether proprioceptive recalibration, like reach adaptation, generalizes to locations at different distances across the workspace. We had subjects adapt their reaches with a rotated cursor to two target

locations (13 cm distance from a home position), and then, we compared how reach aftereffects and changes in proprioceptive estimates generalized to novel locations in the same direction as the trained targets but at different distances (10 and 15 cm from the home position). We found slightly different generalization patterns for proprioceptive recalibration compared to reach adaptation. Specifically, reach aftereffects generalized almost completely to targets at novel locations (i.e., targets closer and farther from the start position relative to the trained target). In contrast, while changes in felt hand position occurred at both trained and novel locations in the workspace, the amount of change was significantly smaller for reference markers located farther from the start position compared to the trained distance.

### Generalization of motor adaptation

Our subjects adapted their reaches when training with the 45° CW rotated cursor and the magnitude of the aftereffects (i.e., changes in reach movements) in this study was around 30 % of the visuomotor distortion which is consistent with previous findings from our laboratory (Salomonczyk et al. 2011; Clayton et al. 2014). Changes in reaching movements following reach training to a single target with a rotated cursor has been found to generalize across different distances in the same direction as the training target (Krakauer et al. 2000; Shabbott and Sainburg 2010). For example, Krakauer et al. (2000) found that visuomotor adaptation following reaches to a single target (7.2 cm from the start position), with 30° CCW rotated visual feedback, fully generalized to three novel targets in the same direction but at different distances than the trained target (2.4, 4.8, and 9.6 cm relative to the adapted distance). In the study by Shabbott and Sainburg (2010), subjects adapted their reaching movements to eight targets located 15 cm away after training with a 30° CW cursor rotation. Results indicated that subjects completely generalized their adapted reaches to novel targets located 22.5 cm away (in the same directions as the trained targets), although the extent of generalization was a bit smaller for a separate group who only received knowledge of results during training. In accordance with these findings, we found that reach adaptation generalized across movement distance such that subjects' open-loop reaches were adapted to a similar extent to the trained, novel-near, and novel-far targets. Conversely, Mattar and Ostry (2010) showed a different generalization pattern in a force-field adaptation study. In their study, two groups of subjects reached to either a 15 or 30 cm target in a velocity-dependent force field. Generalization was then assessed by having subjects reach to a 30 or 15 cm target, respectively. They found that generalization was complete when the novel target was nearer, i.e., 15 cm (thus

overlapped the target distance) but only partial when the novel target was farther, i.e., 30 cm. Based on these results, Mattar and Ostry suggested that dynamic learning is locally tuned to the situation in which it is acquired such that generalization decays after a certain distance from the trained target. Mattar and Ostry (2010) proposed that the inconsistency between their results and the results of Krakauer et al. (2000) arose because their far-novel target was twice as far from the trained target, while Krakauer's novel target was only 33 % farther (novel-far target was 50 % farther in Shabbott and Sainburg's 2010 study). However, using a similar force-field paradigm, Goodbody and Wolpert (1998) found that reach adaptation generalized to novel targets that were twice as far or required twice the speed; specifically, a training distance of 12.5 cm generalized completely to a novel target distance of 25 cm. Thus, it appears that generalization tends to be complete for farther targets, especially following visuomotor rotation adaptation.

The generalization pattern of reach adaptation is quite different when testing novel targets that differ in direction from the trained direction. For example, Pine et al. (1996) found that reach adaptation to a single target resulted in generalization of only ~50 % when reaching to novel targets that deviated by 22.5° from the trained direction. Moreover, only about 20 % of adaptation generalized to novel-untrained targets located 45° from the trained direction. Following the study by Pine et al. (1996), Krakauer et al. (2000) found a slight increment in the percentage of rotation adaptation that generalized to novel target directions (i.e., ~80 % for novel targets located 22.5° and 25 % for novel targets located 45° relative to the trained target). These results demonstrate that generalization is local in direction (the same pattern found by Neva and Henriques (2013)). We also replicated this pattern in a recent study when our subjects showed a limited pattern of generalization to different target directions after visuomotor adaptation with rotated visual feedback of the hand (Cressman and Henriques, in revision).

The generalization pattern seen when reaching to different distances of the workspace in our current study may have arisen due to varying levels of activation in the same neuron population in the adaptation process and no-cursor reaches which facilitated the generalization of adaptation to the novel distances in the same trained direction. It has been hypothesized that visuomotor adaptation to rotation perturbations results in remapping of the hand-centered reference axes which, in turn, shows complete generalization to novel targets in the same direction and limited generalization to novel target directions (Pine et al. 1996; Krakauer et al. 2000). Additionally, according to the neurophysiological properties of motor cortical neurons, Goodbody and Wolpert (1998) explained that scaling a movement, either temporally or in amplitude after adapting to novel

dynamics of a force field, could involve the same population of neurons that were involved in the learning process, broadly activated at a different level. Moreover, it has been demonstrated that generalization is more complete to locations that require activation of the same muscles used during training compared to locations that require recruiting different muscles such as is the case when reaching in one direction with different amplitude requirements (de Ruyg 2010). Therefore, the generalization pattern to different distances of the workspace shown in our study may have involved various levels of activation of the same neuron population that were involved in the adaptation process which facilitated the generalization of adaptation to the novel distances in the same trained direction.

### Proprioceptive acuity across the workspace

Following training with an aligned cursor, our subjects perceived their unseen hand position to be slightly rightward of its actual position. Indeed, with no reach training, the same pattern has been observed previously in our laboratory (Jones et al. 2010, 2012). These studies reported that right-handed participants perceived their right hand to be more rightward than it actually was and the left hand to be more leftward than it actually was. Moreover, we did not find any significant differences between proprioceptive estimates across the novel-near and novel-far locations in this baseline condition, while Wilson et al. (2010) observed a location-dependent pattern such that their subjects estimated their hand position to be less biased for locations closer to the body than locations farther from the body. Of note, in their study, the distance between the near- and far-test locations was 60 % of each subject's maximum reach (MR) (e.g., 39 cm if MR = 65 cm), while this distance in our study was 5 cm and was fixed for all subjects which resulted in observing no significant differences in our baseline data. Thus, differences in the sensitivity of hand proprioception appear to arise only when comparing hand locations quite far from the body (when the arm is mostly extended).

### Generalization of proprioceptive recalibration

Following reach training with misaligned visual feedback of the hand, our subjects also felt their hand position to be shifted to the right of the trained target locations (in the same direction as the visual distortion). Subjects felt hand positions were shifted on average 8.5° relative to baseline levels. This change in felt hand position (i.e., proprioceptive recalibration) replicates previous work from our laboratory (Cressman and Henriques 2009). Moreover, healthy subjects (as well as cerebellar patients) have shown significant shifts in their perceived direction of the out-and-back

movements of their unseen right hand, which they indicated with their opposite left hand following reach training with a rotated cursor with their right hand (Synofzik et al. 2008; Izawa et al. 2012). In addition, other studies have observed changes to subjects' sense of hand motion after reach adaptation to a velocity-dependent force field (Ostry et al. 2010; Vahdat et al. 2011; Mattar et al. 2013).

Our study shows that proprioceptive recalibration generalizes across novel locations at different distances of the workspace; however, the extent of generalization depends on the distances of the reference markers relative to the training target location. Here, we suggest a distance-dependent generalization for proprioceptive recalibration, due to the fact that the subjects (in the training tasks) have experience with the visual–proprioceptive discrepancy of novel-near locations while reaching to the training locations. This may have influenced subject's estimates at the novel-near locations stronger than for the novel-far locations where no such sensory discrepancy is experienced. This is in contrast, for the reach adaptation (generalize equivalently for near and far targets) where cross-sensory discrepancy may play less of a role in this change in motor command (Henriques and Cressman 2012).

Cressman and Henriques (in revision) also attempted to investigate the generalization pattern of changes in felt hand position across different directions in the workspace (following visuomotor adaptation). Specifically, they had subjects adapt their reaches to a single target with a 45° CW rotated cursor and then they compared proprioception estimates at locations across the workspace relative to the trained target location (i.e., assessed proprioceptive recalibration at locations 45° and 90° away from trained target direction). Results showed that sense of felt hand position shifted by a similar amount (i.e., 6°–7°) both in the trained and novel directions. In contrast to this broad generalization across direction, we found that changes in felt hand position were significantly smaller for the novel-far compared to the trained distance. The difference between proprioceptive recalibration generalization patterns across the two studies suggests that proprioceptive information regarding the extent and direction of the hand movement is processed differently in the brain.

### Different generalization patterns for reach adaptation and proprioceptive recalibration

Our results show that generalization patterns for reach adaptation and proprioceptive recalibration are influenced by the coordinates of the novel (testing) locations (e.g., distance relative to the trained location) in the work space. In the present study, the changes in reaching movements generalized to the same extent to all targets located at different distances but the same direction as the training

targets. In contrast, Cressman and Henriques (in revision) showed that reach adaptation showed limited generalization such that generalization was local to the trained direction compared with novel targets located in different directions. The generalization patterns for proprioceptive recalibration differed from reach adaptation in both studies. Specifically, in the current study, the changes in felt hand position were significantly smaller for the novel-far compared to the trained distance, but changes in felt hand position generalized to all novel directions in Cressman and Henriques study. Moreover, in a recent study, we found that proprioceptive recalibration was specific to the hand exposed to the visual distortion such that recalibration did not transfer to the untrained hand while changes in reaches partially transferred (i.e., to the untrained non-dominant hand) (Mostafa et al. 2014). These results provide further evidence in support of the proposal that proprioceptive recalibration may arise independently of changes in the motor system.

### In summary

Our results showed that following visuomotor adaptation, reach aftereffects generalized to both near-novel and far-novel targets distances, while proprioceptive recalibration was significantly smaller for the far marker locations. These results should be taken into consideration when designing motor rehabilitation programs for individuals suffering from neurological disorders, and/or when establishing experimental sensorimotor tasks to study motor and sensory changes, which occur in motor learning.

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