

## CHAPTER 6

# Motor adaptation and proprioceptive recalibration

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**Abstract:** Goal-directed reaches are rapidly adapted after reaching with misaligned visual feedback of the hand. It has been suggested that reaching with misaligned visual feedback of the hand also results in proprioceptive recalibration (i.e., realigning proprioceptive estimates of hand position to match visual estimates). In this chapter, we review a series of experiments conducted in our lab which examine this proposal. We assessed proprioceptive recalibration by comparing subjects' estimates of the position at which they felt their hand was aligned with a reference marker (visual or proprioceptive) before and after aiming with a misaligned cursor that was typically rotated 30° clockwise (CW) with respect to the hand. In general, results indicated that subjects recalibrated proprioception such that their estimates of felt hand position were shifted in the same direction that they adapted their reaches. Moreover, proprioception was recalibrated to a similar extent of motor adaptation (~30%), regardless of how the hand was positioned during the estimate trials (active or passive placement), the location or modality of the reference marker (visual or proprioceptive), the hand used during reach training (right or left), how the distortion was introduced (gradual or abrupt), and age (young or older subjects) and the magnitude of the visuomotor distortion introduced (30° or 50° or 70°). These results suggest that in addition to recalibrating the sensorimotor transformations underlying reaching movements, visuomotor adaptation results in partial proprioceptive recalibration.

**Keywords:** visuomotor adaptation; sensory recalibration; proprioception.

## Introduction

When reaching to visual targets, one uses vision and proprioception to plan movements (e.g., Jeannerod,

1988). If these sensory cues conflict and one is reaching to a visual target, one tends to rely more on the visual estimate of the hand than on the actual or felt position. For example, it has been shown that when reaching to a target with misaligned visual feedback of the hand (i.e., reaching in a virtual reality environment or while wearing prism goggles), one adjusts the movement in order for the visual

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representation of the hand to achieve the desired endpoint (Baraduc and Wolpert, 2002; Ghahramani et al., 1996; Klassen et al., 2005; Krakauer et al., 1999, 2000; Magescas and Prablanc, 2006; Redding and Wallace, 1996; Simani et al., 2007; Vetter et al., 1999; Wang and Sainburg, 2005). This process is referred to as visuomotor adaptation and results in the formation of a new visuomotor mapping to guide one's movements.

In the research presented below, we examine how the brain deals with conflicting sensory signals during visuomotor adaptation. Based on changes observed in the motor system, it has been proposed that changes in reaches arise after reaching with misaligned visual feedback of the hand due to a difference between the desired (predicted) and actual sensory feedback arising from a given motor command. For example, when first reaching with altered visual feedback of the hand, one expects to see the visual representation of the hand head to the target. However, because visual feedback of the hand is misaligned from the actual hand location, the hand is seen to head off on an angle. This gives rise to an error signal, and it is thought that this signal (i.e., the sensory discrepancy between the predicted and actual sensory feedback) is used to amend the motor command (Miall and Wolpert, 1996; Wolpert, 1997; Wolpert et al., 1995).

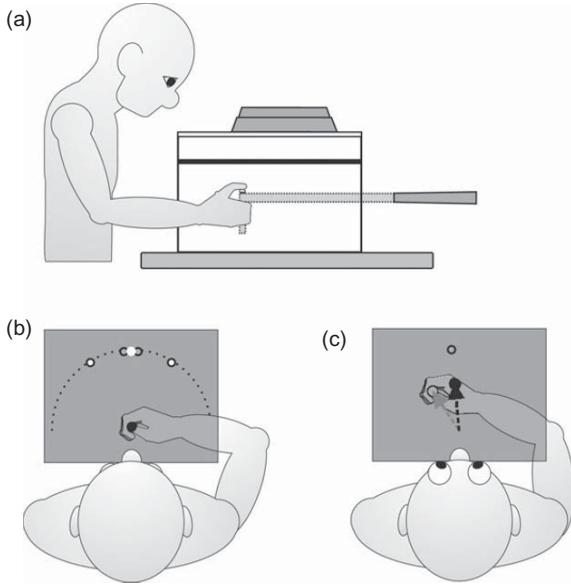
While models accounting for motor learning include a role for sensory feedback, it is unclear what happens to one's sense of felt hand position during motor learning. How does the brain resolve the spatial conflict between seen and felt hand location? To look at this issue, we (1) asked if proprioceptive estimates of felt hand position are remapped (i.e., recalibrated) to match the visual representation of one's hand and (2) examined whether changes in proprioception contribute to changes in one's reaches. Previous research examining sensory recalibration has typically asked subjects to reach to visual and proprioceptive targets with their adapted hand following visuomotor adaptation (Harris, 1963; Hay and Pick, 1966; Simani et al., 2007; van Beers et al., 2002). While subjects' reaches are altered

following visuomotor adaptation, it is unclear if these changes reflect sensory recalibration (specifically proprioceptive recalibration) *per se*. Subjects were allowed to freely move their adapted arm. Thus errors in reaches could have arisen because subjects were using the adapted sensorimotor mapping to program their movements. In the research discussed below, we examined sensory recalibration by determining changes in felt hand position following visuomotor adaptation in perceptual, nonreaching tasks. Specifically, proprioceptive estimates of hand position were measured in a task, in which subjects did not reach, aim, align—or otherwise freely move—their adapted hand to a target (i.e., subjects did not complete a goal-directed movement). Thus, these proprioceptive estimates provide insight into sensory recalibration processes, independent of possible motor changes.

To start, we will provide a general description of our proprioceptive estimation task and then outline the visuomotor tasks subjects completed before we assessed felt hand position. Overall, our results indicate that proprioception is recalibrated following visuomotor adaptation. As well, our results begin to reveal the relationship between sensory plasticity and adaptation of motor commands.

## General methodology

We assessed changes in subjects' felt hand position by determining the position at which they perceived their hand to be aligned with a reference marker. On proprioceptive estimation trials, subjects grasped the handle of a robot manipulandum (Interactive Motion Technologies; Fig. 1a) and pushed it out from the home position along a robot-generated constrained linear path (i.e., a slot) to a location somewhere along the dotted line shown in Fig. 1b. If subjects attempted to move outside of the established path, the robot generated 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)) perpendicular to the linear path (Henriques and Soechting, 2003; Jones et al., 2010).



**Fig. 1. Experimental setup and design.** (a) Side view of the experimental setup. (b and c) Top view of experimental surface. (b) In general, reach targets (open black circles) and reference markers (filled white circles) used in the proprioceptive estimation task were located along a circular arc, 10 cm from the home position (black filled circle). Note that the black dotted line is provided as a reference to indicate the locations of the targets and reference markers and illustrate potential positions that the hand could have been moved to during the proprioceptive estimation trials. (c) Possible visuomotor distortion introduced in the reach training task when subjects reached with a misaligned cursor. In this example, the black cursor (representing the hand) was rotated 30° clockwise with respect to the actual hand location.

Once the hand reached its final position, a reference marker appeared (e.g., white circles in Fig. 1b, from Cressman et al., 2010) and subjects made a two-alternative forced-choice judgment about the position of their hand (left or right) relative to the reference marker. Because subjects actively moved their hand into position by pushing the robot handle out along a constrained path, we refer to these estimation trials as active placement estimates. As discussed below, one of the first questions we asked with respect to proprioceptive recalibration was whether shifts in

subjects' felt hand position were dependent on how their hand was moved into position. Specifically, we asked if changes in subjects' felt hand position differed depending on whether subjects actively moved the robot handle into position (active placement estimates) or the robot passively moved subjects' hands into position along the same constrained path (passive placement estimates). In general, results reported are from active placement estimate trials, unless otherwise noted.

To determine the locations at which subjects felt their hand was aligned with a reference marker, we adjusted the position of the hand with respect to each reference marker over proprioceptive estimation trials (50 for each reference marker) using an adaptive staircase algorithm that was dependent on a subject's pattern of responses (Cressman and Henriques, 2009; Kesten, 1958; Treutwein, 1995). We then fit a logistic function to each subject's left-right responses for each reference marker for each testing session that they completed (Cressman and Henriques, 2009, 2010a; Cressman et al., 2010; Jones et al., 2010). Based on each logistic function, we calculated the bias (accuracy: the point of responding left (or right) 50% of the time) and uncertainty (precision: the difference between the values at which the response probability of responding left (or right) was 25% and 75%).

In general, we measured proprioceptive estimates of hand position after subjects trained to reach to targets with a free-moving robot manipulandum (i.e., the robot's motion was not constrained to a specific path as in the proprioceptive estimation trials). In the first training session, subjects freely reached to targets with a cursor that was aligned with the hand. In the second training session, subjects reached to targets with a misaligned cursor, for example, a cursor that was either gradually or abruptly rotated CW with respect to the hand. To introduce the distortion gradually, the cursor was aligned with the hand on the first reaching trial. Over

subsequent trials, the cursor was rotated CW with respect to the hand in increments of  $0.75^\circ$  until the goal distortion was achieved (typically  $30^\circ$ ). In testing sessions in which the distortion was introduced abruptly, the cursor was rotated  $30^\circ$  CW with respect to the hand on the first reaching trial. Details regarding the order of the reach and proprioceptive estimation trials for each of the two testing sessions are provided in Fig. 2. To assess the extent of motor adaptation (or motor recalibration), subjects reached to targets without any visual feedback of their hand (i.e., without a cursor) so that we could measure reach aftereffects (i.e., changes in reach errors).

### ***Proprioception is recalibrated following visuomotor adaptation***

In all of our studies to date (Cressman and Henriques, 2009, 2010a; Cressman et al., 2010), we have consistently found proprioceptive recalibration at all reference marker locations following visuomotor adaptation. An example of such findings from a recent study (Cressman et al., 2010) is shown in Fig. 3. Here, proprioceptive estimates were shifted  $6^\circ$  more left after reach training with a cursor that was gradually rotated  $30^\circ$  CW with respect to the hand (black squares in Fig. 3a) compared to estimates obtained after reaching with

an aligned cursor (black triangles in Fig. 3a). Further, from Fig. 3b, we see that these shifts in proprioceptive estimates were in the same direction that subjects adapted their reaches. We found similar changes in proprioceptive estimates of hand position (i.e., shifts of  $6^\circ$ ) when the robot passively moved the hand into position during the estimation trials (Fig. 4, passive placement estimates (filled black circles) vs. active placement estimates (open white circles); Cressman and Henriques, 2009). As well, changes in proprioceptive estimates generalized to novel locations at which subjects did not have any practice reaching to (i.e., reference markers that were deviated  $15^\circ$  from the reach targets during training with the aligned or misaligned cursor (data not shown; Cressman and Henriques, 2009)). However, at all reference markers, proprioception was only recalibrated a fraction (about one-third) of the extent that subjects adapted their reaches (Cressman and Henriques, 2009; Cressman et al., 2010), regardless of whether subjects actively moved their hand along a constrained path or the robot passively moved the hand into position during the proprioceptive estimate trials.

In addition to finding proprioceptive recalibration in the right hand, we have also found similar shifts in felt hand position of the left hand, after subjects trained with the left hand (Salomonczyk et al., 2010a). In fact, the only difference between

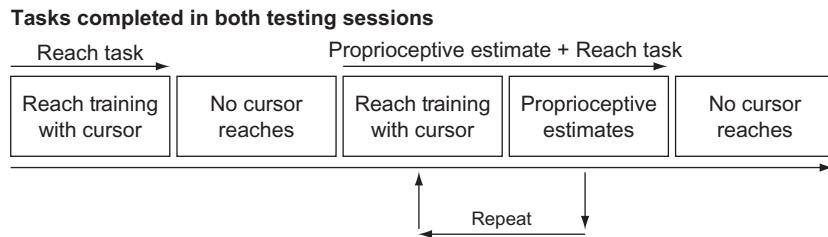


Fig. 2. Schematic showing the order in which different tasks were typically completed within a testing session. In the first testing session, subjects reached with an aligned cursor on all reach training trials. On the second day of testing, the cursor was misaligned from the actual hand location (e.g., rotated clockwise with respect to the actual hand location, Box 1). After the visually guided reach training trials, subjects next reached to the reach targets without a cursor to assess motor adaptation (No cursor reaches, Box 2). This was followed by interleaving proprioceptive estimation trials (Box 3) and visually guided reaches (Box 4). Finally, subjects completed an additional set of no cursor reaches to end the testing session (Box 5).

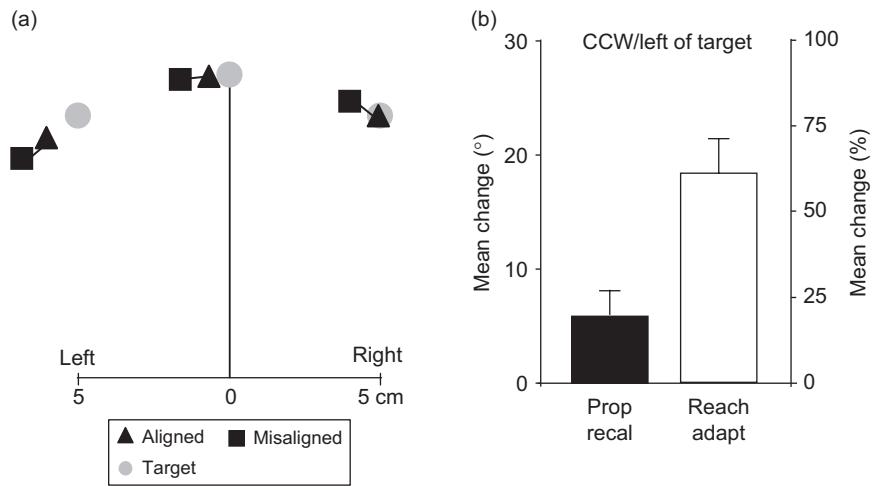


Fig. 3. (a) Mean 2D biases on the proprioceptive estimation task after subjects reached with an aligned (triangles) or misaligned (squares) cursor during the reach training task. In (b), we show mean changes in proprioceptive estimates (black bar) and reach errors (i.e., motor adaptation, white bar) after subjects reached with a misaligned compared to aligned cursor. Results are shown in degrees and as a percentage of the distortion introduced during reach training trials. Error bars reflect standard error of the mean (from Cressman et al., 2010).

the right and left hand proprioceptive estimates was a hand-dependent bias in estimated position, such that right-hand biases were more left of a reference marker than left-hand biases. These results are consistent with work from our lab in which we specifically compared proprioceptive acuity between the two hands and found that, in general, subjects judged their left hand to be more left than it actually was and their right hand to be more right than it actually was (Jones et al., 2010).

Having established that proprioception was recalibrated in the trained hand (either right or left) with respect to a visual reference marker, we then determined if this change in hand position reflected an overall shift in felt hand position. To do this, we manipulated the modality of the center reference marker such that subjects estimated the position of their hand with respect to body midline (i.e., a proprioceptive reference marker). We found shifts in the position at which subjects perceived the hand was aligned with the proprioceptive reference marker that were similar in magnitude and direction to the shifts observed when a visual reference

marker was displayed at the same location (Cressman and Henriques, 2009). Given that we found that hand-reference marker alignment biases were shifted regardless of reference marker modality (i.e., regardless of whether the reference marker was an extrinsic cue (a visual reference marker) or an intrinsic, egocentric cue (the body midline)), our results suggest that proprioception is recalibrated such that there is a general shift in felt hand position as opposed to a visual–proprioceptive realignment. This shift is only evident in the trained hand (i.e., the hand that performs the reaching trials), as we did not find evidence of proprioceptive recalibration in the untrained (left or right) hand (Salomonczyk et al., 2010a).

#### ***Proprioceptive recalibration is not dependent on motor learning conditions***

Given differences in reaching errors to visual and proprioceptive targets following prism exposure, it has been suggested that the sensory processes

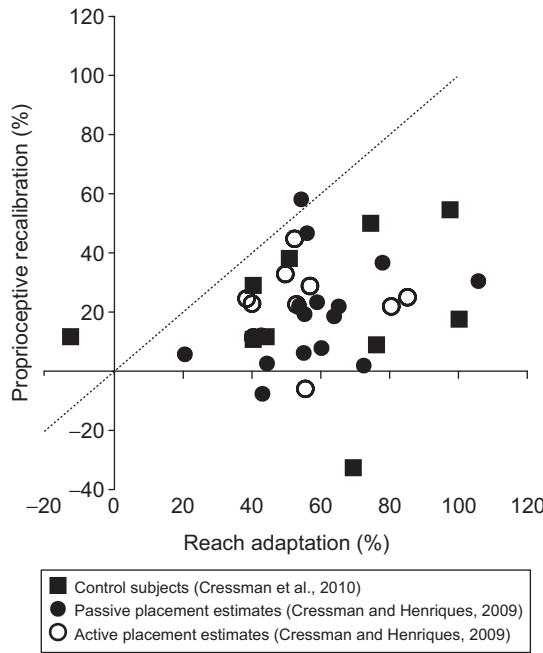


Fig. 4. The changes in proprioceptive estimates are plotted as a function of changes in reach aftereffects for each subject after training with a misaligned cursor compared to an aligned cursor. Results are shown for (1) the control (i.e., young) subjects in Cressman et al. (2010) and (2) subjects from Cressman and Henriques (2009), when the robot positioned their hands during the estimation trials (passive placement estimates, filled black circles) and when they actively moved their hand into position (active placement estimates, open white circles). The dashed line is a unit slope and thus indicates equivalent levels of proprioceptive recalibration and motor adaptation.

engaged during visuomotor adaptation are dependent on how the visuomotor distortion is introduced (i.e., gradual vs. abrupt) and age (Bock, 2005; Bock and Girgenrath, 2006; Heuer and Hegele, 2008; McNay and Willingham, 1998; Redding and Wallace, 1996; Redding et al., 2005). In particular, it has been suggested that strategic, cognitive processes are engaged early during the learning process when a visuomotor distortion is introduced abruptly to produce rapid corrections in motor performance (Redding and Wallace, 1996; Redding et al., 2005). Moreover,

it is proposed that older individuals have difficulty engaging these processes, leading to motor learning deficits (Bock, 2005; Bock and Girgenrath, 2006). In contrast, spatial realignment processes (i.e., proprioceptive recalibration) are thought to be responsible for motor adaptation when a visuomotor distortion is introduced gradually, and these processes are proposed to be maintained with advancing age (Heuer and Hegele, 2008; McNay and Willingham, 1998; Redding and Wallace, 1996).

While motor adaptation results indicate differences in performance depending on processes engaged during motor learning, our results indicate that this is not the case when assessing estimates of hand position. We found no change in our estimate results: proprioception was consistently recalibrated and recalibrated to a similar extent ( $\sim 6^\circ$ ), regardless of whether the distortion was introduced gradually or abruptly (Salomonczyk et al., 2010a). This similarity was found despite the fact that there was some decay in reaching errors (i.e., motor adaptation) over time following reach training when the distortion was introduced abruptly.

To begin to investigate the influence of age-related changes in motor learning on proprioceptive recalibration, we had a group of elderly subjects (mean age = 66.3, SD = 6.0 years) adapt to a gradually introduced visuomotor distortion and then complete our proprioceptive estimation task (Cressman et al., 2010). Results revealed that elderly subjects recalibrated proprioception to the same extent as younger (i.e., control) subjects ( $\sim 6^\circ$  left of the marker). These results indicate that proprioception is recalibrated to a similar extent throughout the lifespan, when a visuomotor distortion is introduced gradually and similar levels of motor adaptation are achieved. Taken together, these results indicate that sensory recalibration processes are similar regardless of how a visuomotor discrepancy is introduced and one's age. These results, as determined by our proprioceptive estimation task, do not follow the same trend as reaching results

(achieved in the prism literature), suggesting that sensory and motor changes may be two independent processes arising from visuomotor learning.

### ***The relationship between proprioceptive recalibration and motor adaptation***

As shown in Fig. 4, we found that (1) almost all subjects recalibrated proprioception to some extent following visuomotor adaptation; (2) in almost all instances, proprioceptive recalibration was less than motor adaptation; and (3) the magnitude of proprioceptive recalibration was similar regardless of the level of motor adaptation achieved. In accordance with this last observation, our results to date have not revealed a significant correlation between the magnitude of proprioceptive recalibration and the level of motor adaptation attained, as measured in open-loop reaches with no cursor feedback (Cressman and Henriques, 2009; Cressman et al., 2010). These results further suggest that proprioceptive recalibration and motor adaptation may be two independent processes arising after training with misaligned visual feedback of the hand.

To investigate the relationship between proprioceptive recalibration and motor adaptation in more detail, we manipulated the extent of motor adaptation achieved by changing the magnitude of the cursor distortion on the reach training trials. Specifically, we examined changes in sense of felt hand position with increasing levels of motor adaptation (Salomonczyk et al., 2010b). To increase levels of motor adaptation, we had subjects complete three testing sessions with a rotated cursor. In the first session, the cursor was gradually rotated 30° CW with respect to the hand during the reach training trials. In the second session, the distortion was increased to 50° and then finally to 70° in the third session. We found that motor adaptation increased in the expected direction over reach training blocks. Subjects reached on average 16° more left of the target after training with a 30° CW rotated cursor

compared to an aligned cursor. These reach errors increased to 27.6° and 33.8° after training with a 50° CW rotated cursor and 70° CW rotated cursor, respectively, compared to training with an aligned cursor. Similar to this increase in motor adaptation, we found that proprioception was also recalibrated to a greater extent following reach training with increasing visuomotor distortions (from 7° after reach training with a 30° rotated cursor to 12° after training with a 50° cursor to 15° after training with a 70° cursor). However, even though both motor and sensory processes were adapted to a greater extent across the experiment, motor adaptation was approximately 50% of the visuomotor distortion across all blocks of trials and proprioceptive recalibration was maintained at a constant percentage of motor adaptation (~40%, or about 20% of the visuomotor distortion introduced). While the magnitude of the visuomotor distortion was correlated with both changes in movement aftereffects and proprioceptive bias, no significant correlation between these motor and sensory changes was observed overall or within training blocks. Thus it appears that while sensory recalibration and motor adaptation do occur simultaneously and are similarly affected by the size of distortion (and thus the size of the respective error signals), the mechanisms underlying these processes may arise independently following visuomotor adaptation.

Taken together, our findings suggest that when one learns a new visuomotor mapping, one also recalibrates proprioception in the trained hand (Salomonczyk et al., 2010a). In accordance with our results, Ostry and colleagues (2010) have recently reported changes in felt hand position after subjects learned to reach in a velocity-dependent force field. Similar to our results, they found that proprioception was recalibrated to about 33% of motor adaptation. Thus this consistency in proprioceptive recalibration is found regardless of reaching task (i.e., visuomotor distortion vs. velocity-dependent force field), how the hand is positioned during the estimate trials

(active vs. passive placement), the location or modality of the reference marker (visual or proprioceptive), the hand used during reach training (right vs. left), how the distortion is introduced (gradual vs. abrupt), age (young vs. older subjects), and the magnitude of the visuomotor distortion introduced ( $30^\circ$  vs.  $50^\circ$  and  $70^\circ$ ).

It is important to keep in mind that these changes in the estimate of felt hand position are only a fraction of the motor learning-related changes observed in the unseen trained hand (i.e., motor adaptation). Thus it is unlikely that sensory recalibration is the sole source driving adaptive changes in reaching movements. In fact, given that sensory and motor adaptation are differentially influenced by the processes engaged during reach training (i.e., strategic vs. realignment processes) and that we have found no significant correlation between changes in these systems, sensory and motor changes could be two independent processes. This proposal is supported by studies that have demonstrated motor adaptation in the absence of proprioceptive recalibration, for example, deafferented individuals have been shown to adapt their reaches in response to altered visual feedback of the hand (see Bernier et al., 2006; Ingram et al., 2000; Miall and Cole, 2007). As well, Henriques and colleagues have shown that under some conditions in which motor adaptation is observed, subjects do not recalibrate their sense of hand path geometry (Wong and Henriques, 2009) or path length (Cressman and Henriques, 2010b).

To determine the relationship between proprioceptive recalibration and motor adaptation in more detail, we are now investigating how sensory and motor changes generalize to different areas of the workspace. Specifically, we are asking if proprioceptive recalibration extends from a final position (e.g., at the distance of the target) to other positions along the trajectory and how this relates to observed changes in reach trajectories at these positions. Answers to this question may also help explain why we did not find evidence of proprioceptive recalibration

when subjects had to assess a path's shape or length. Moreover, we are looking to see if proprioceptive recalibration generalizes across the workspace after a subject reaches to just one target with a misaligned cursor. Work by Krakauer et al. (2000) suggests that motor adaptation can be limited to certain areas of the workspace after subjects train to just one target. We will look to determine if proprioceptive recalibration follows the same trend.

For now, our results suggest that proprioception regarding final endpoint position is recalibrated under task conditions in which motor learning arises. It remains to be determined if motor adaptation and proprioceptive recalibration are two independent adjustments arising from learning to reach with misaligned visual feedback of the hand.

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