Generalization of Motor and Sensory Changes in Motor Learning

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Abstract

This dissertation examines the generalization of motor and sensory changes in motor learning. Chapter two describes the process of intermanual transfer of reach adaptation and proprioceptive recalibration. We exposed participants to a laterally translated cursor while reaching with one hand to three targets, and then we measured reach aftereffects and changes in felt hand position for the trained and untrained hand. We found reach adaptation transfer from right to left hand and no transfer of proprioceptive recalibration. This suggests that the intermanual transfer for motor adaptation is hand-dependant, and proprioceptive recalibration is specific to the trained hand. Chapter three describes the generalization patterns of reach adaptation and proprioceptive recalibration across different distances. Reach aftereffects and changes in estimates of hand position were measured following reach-training with a rotated visual feedback of the hand to a single target distance. We found that reach adaptation and proprioceptive recalibration transfer across near and far novel distances. However, proprioceptive recalibration generalization was significantly smaller at far novel locations. This suggests that, unlike motor adaptation, the extent of sensory changes generalization is distance-dependent. Chapter four describes the contribution of proprioceptive recalibration and updated efference-based sensory predictions in motor adaptation and changes in hand localization. We exposed our participants to only visual-proprioceptive discrepancy by removing volitional movements and having a robot move their hand passively. Then, we examined changes in hand localization in two hand movement conditions, i.e., active (self-generated) and passive (robot-generated). Results showed no significant difference in hand localization changes between active and passive conditions. This suggests changes in hand localization reflect mainly proprioceptive recalibration of the hand rather than updates in efference-based sensory predictions, and entirely on proprioceptive recalibration when training does not include any volitional movements. Additionally, in Chapter four, we examined how reach adaptation and proprioceptive recalibration generalized across different directions in the workspace. We found that reach aftereffects generalized to neighboring novel targets in a pattern similar to proprioceptive recalibration generalization pattern. This suggests that some of the reach adaptation reflect proprioceptive changes. Our findings provide insight into the characteristics of proprioceptive recalibration and how this process influences motor learning. This should be taken into consideration when designing motor adaptation/learning paradigms, teaching a motor skill or designing a movement rehabilitation protocol.

For my Dad and Mom

إلى أصحاب الفضل والعطاء بلا مقابل

أبي و أمي

عادل صبري و ثريا السعيد

أدعو الله لكما بدوام الصحة والعافية

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 Background

Giving the constant changes in our body and the surrounding environment, the ability to adapt to such changes is a key process. *Motor adaptation* is a type of motor learning which involves remapping the relationship between sensory information (visual and proprioceptive) and motor commands following perturbations (Tanaka, 2010). Motor adaptation is very crucial to the motor system for maintaining stability and control of everyday movements. The central nervous system (CNS) evolved this kind of plasticity to deal with both body-growth changes and variability in the surrounding world. Studies of motor adaptation have a long history, spanning for more than a century. Stratton (1897) investigated how inverted vision, obtained by wearing prism glasses, could be remapped with body movements over time. In one of his experiments, for eight days, he wore prism glasses that inverted the visual field vertically. It was strange and difficult for him to move during the first four days, but, on day five he started to be able to move normally while vision was inverted. Even for complex movements, such as riding a bicycle, participants were able to adapt and ride a bicycle within 30 days of wearing prism goggles. For smaller prism displacements, such as those that shift the visual field by 11.3 degrees, adaptation to reaching or throwing movements is much quicker and can occur within an hour of training (Redding, Rossetti, & Wallace, 2005). To date, many laboratories have further showed the elegant ability of humans to adapt their movements to a wide range of visuomotor alterations.

In the past couple of decades, researchers have been investigating motor (or reach) adaptation, using virtual reality setups, by kinematically altering the visual feedback of the hand (a cursor that represents the hand), while participants reach to visual targets in the workspace. In this method, the cursor could be either rotated or translated relative to the hidden, trained hand, to introduce a small discrepancy between the visual feedback of the hand and the actual hand. In this way, unlike prism adaptation, only the visual motion of the hand is affected and not the background nor target location (Krakauer, Ghilardi, & Ghez, 1999). Typically, during this type of training, participants adapt their reaches in order to get the cursor on the target while the actual hidden hand is directed off-target. Reach adaptation during these tasks can be represented by a learning curve, which shows the gradual adjustments to reach trajectories and reach-errors reduction behavior until the end of training. Additionally, after sufficient training, the reaches continue to deviate after the cursor (and thus any vision of the hand) is removed entirely or if the perturbation is removed. These persistent reach deviations are known as reach aftereffects. In this dissertation, we will examine motor adaptation by measuring reach aftereffects following training with a variety of perturbations.

Visuomotor adaptation also produce consistent, although sometimes limited, generalization. That is, adaptation while training with one hand and to one location in the workspace can transfer partially to the opposite hand or generalize to other novel locations across the workspace (Imamizu, Uno, & Kawato, 1995; Krakauer, Pine, Ghilardi, & Ghez, 2000; Pearson, Krakauer, & Mazzoni, 2010; Wang & Sainburg, 2005). Intermanual transfer depends on which hand is trained. Some studies have shown symmetric transfer between hands while others have shown that transfer occurs from one hand to another but not vice versa. Generalization of visuomotor adaptation across different locations on the workspace has shown to be influenced by the type of introduced distortion (i.e., cursor gain or rotation) and the coordinates of the targets in the workspace (i.e., target distances and directions relative to the start position and trained target). For instance, reach adaptation to a cursor rotation to a single target leads to a local or narrow generalization pattern across novel-untrained directions, while adaptation to a cursor gain leads to wider generalization (Krakauer et al., 2000).

Studies have shown that visuomotor adaptation leads not only to motor changes, but also to changes in the felt position of the hand, i.e., proprioceptive recalibration (Cameron, Franks, Inglis, & Chua, 2012; Cressman & Henriques, 2010, 2011; Cressman & Henriques, 2009). When participants are asked to localize the position of their unseen hand following visuomotor training, they estimate their hand to be partially shifted in the direction of the perturbed visual feedback of the hand. To date, proprioceptive recalibration has been observed consistently following different types of distortions (i.e., rotation vs. lateral displacement of hand cursor, Cameron, Franks, Inglis, & Chua, 2012; Cressman & Henriques, 2009), both when the distortion is introduced gradually or abruptly (Salomonczyk, Henriques, & Cressman, 2012), for large as well as small distortions (Salomonczyk, Cressman, & Henriques, 2011), and for younger as well as older adults (Cressman, Salomonczyk, & Henriques, 2010). Furthermore, this change in proprioception has been found to emerge quite quickly; after a dozen reach training trials (Ruttle, Cressman, ’t Hart, & Henriques, 2016). This perceptual change, or sensory plasticity, has been found to be different in size and in patterns of changes from motor output (such as reach aftereffects). Moreover, even when training with a visual-proprioceptive discrepancy of the hand that occurs without volitional movements, as when the robot moves the hand passively, hand proprioception shifts by a similar amount to that produced when the reaching is generated by the participant (Cressman & Henriques, 2010). In addition, reach aftereffects also emerge, and resemble proprioceptive shifts, following this passive-exposure training. This suggests that proprioceptive recalibration plays an important role in sensorimotor learning.

Much remains to be understood about the proprioceptive recalibration process and its characteristics. The purpose of the current dissertation is to examine how both motor and sensory changes generalize between hands and across the workspace following visuomotor adaptation.

Additionally, here I investigate visually-induced changes in hand localization based on efferent signals, as well as proprioceptive signals. The findings will provide insight into how changes in estimates of hand motion emerge and contribute to motor learning and generalization.

This Chapter will provide the reader with some background information that will help to understand the experiments in later Chapters. Proprioception, its neural mechanisms and how it is measured will be explained. Error-based learning and the use of error signals in motor adaptation will then be introduced, with an emphasis placed on the role of proprioceptive recalibration in motor learning. The generalization process of reach adaptation and relevant research findings will then be discussed. Finally, the objectives and rationales of dissertation experiments will be stated.

1.2 Proprioception

To perceive and interact with the environment, our brain processes sensory inputs from several senses. Sherrington (1907) suggested the terms exteroceptors, interoceptors, and proprioceptors to refer to sense organs that provide sensory information, about our body and/or the surrounding world, to the CNS. The exteroceptors were defined as the organs which detect information originating out of the body and included the eyes, ears, mouth, and skin. These organs are designed to extract different types of perceptible energy from the environment (e.g., visible light waves, audible sound waves, etc) and transduce them to electrical signals that are conducted by neurons, through specific neural pathways, and projected to specific cortical areas in the brain. Interoceptors, convey the internal state of the body (such as blood pressure and oxygen concentrations) to the CNS. Proprioceptors are sensory receptors that provide detailed and continuous information to the CNS about the position and motion of the limbs or other segments of the body. This ability to sense position and motion of body segments is known as proprioception. The main proprioceptors for sensing limb motion include muscle spindles, Golgi tendon organs, and joint receptors. Muscle spindles appear to play the dominant role in informing body position and movement, as illustrated by illusions produced by tendon vibration, and deficits produced after loss of sensory neurons bringing input into the CNS, known as deafferentation (reviewed here, Proske & Gandevia, 2012). Proprioception is also facilitated by cutaneous information.

Muscle spindles are composed of numerous intrafusal muscle fibers (Figure 1.1) that are located within the muscle body and change in length along with extrafusal muscle fibers that generate limb movements. As depicted in the figure, an intrafusal muscle fiber is divided into nuclear chain and nuclear bag fibers (1 and 2). Dynamic and static gamma motoneurons innervate nuclear bag 1 fibers, and nuclear chain and nuclear bag 2 fibers, respectively. Afferent information is transmitted from muscle spindles to the CNS by primary Ia and secondary II afferent neurons (Matthews, 1977).

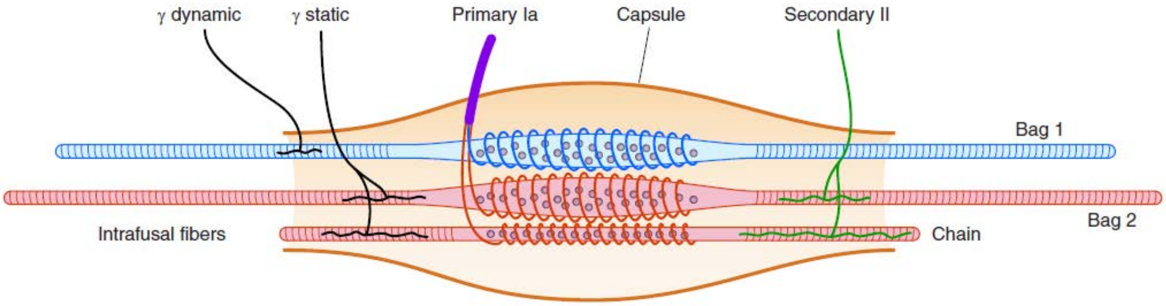

Figure 1.1 Mammalian muscle spindle. The intrafusal fibers include the large nuclear bag 1 and bag 2 fibers together with the smaller nuclear chain fibers. Primary endings, Ia afferent fibers, make terminations around the three intrafusal fiber types. II afferent fibers terminate as secondary endings, supply bag 2 and chain fibers. Gamma static motor neurons innervate bag 2 and chain fibers, while gamma dynamic motor neurons innervate bag 1 fibers (copied from (Proske & Gandevia, 2012))

Golgi tendon organs are encapsulated structures and found in muscle tendons of striated extrafusal muscles, they are also proprioceptive sensory receptors that provide information about muscle tension to the CNS. Golgi tendon organs capsule contain collagen fibers that are connected to a group of muscle fibers. A single Ib afferent fiber innervates one capsule and branches inside into several fine endings that are weaved through collagen fibers. When Golgi organ is stretched the collagen fibers become straightened, thus compressing the Ib nerve endings and causing them to fire (Gilman, 2002).

Sensory inputs from proprioceptors, as cutaneous or tactile, receptors are conveyed by ascending sensory tracts to CNS via the dorsal column (Figure 1.2). Unconscious proprioception pathways primarily terminate in the ipsilateral cerebellum. Conscious proprioception, however, is communicated by the dorsal column-medial lemniscus pathway to the cerebrum, particularly to the somatosensory cortex. These sensory pathways are important for transmitting proprioceptive information necessary for coordinating and performing smooth movements as well as maintaining normal muscle tone and posture. The dorsal column-medial lemniscus pathway begins with proprioceptors (and cutaneous receptors) entering the spinal cord via the dorsal roots, and then project onto neurons within the dorsal root of the spinal cord which axons ascend to the medulla where they synapse onto the second order neurons in the nucleus cuneatus (for upper body) and nucleus gracilis (for lower body). The axons of these neurons (which make up the medial lemniscus) cross the midline and travel to the thalamus, where they synapse onto neurons in the ventral posterolateral nucleus (VPL). This third order neuron relays afferent signals to the postcentral gyrus (i.e., the somatosensory cortex). The somatosensory cortex is arranged in a somatotopic manner.

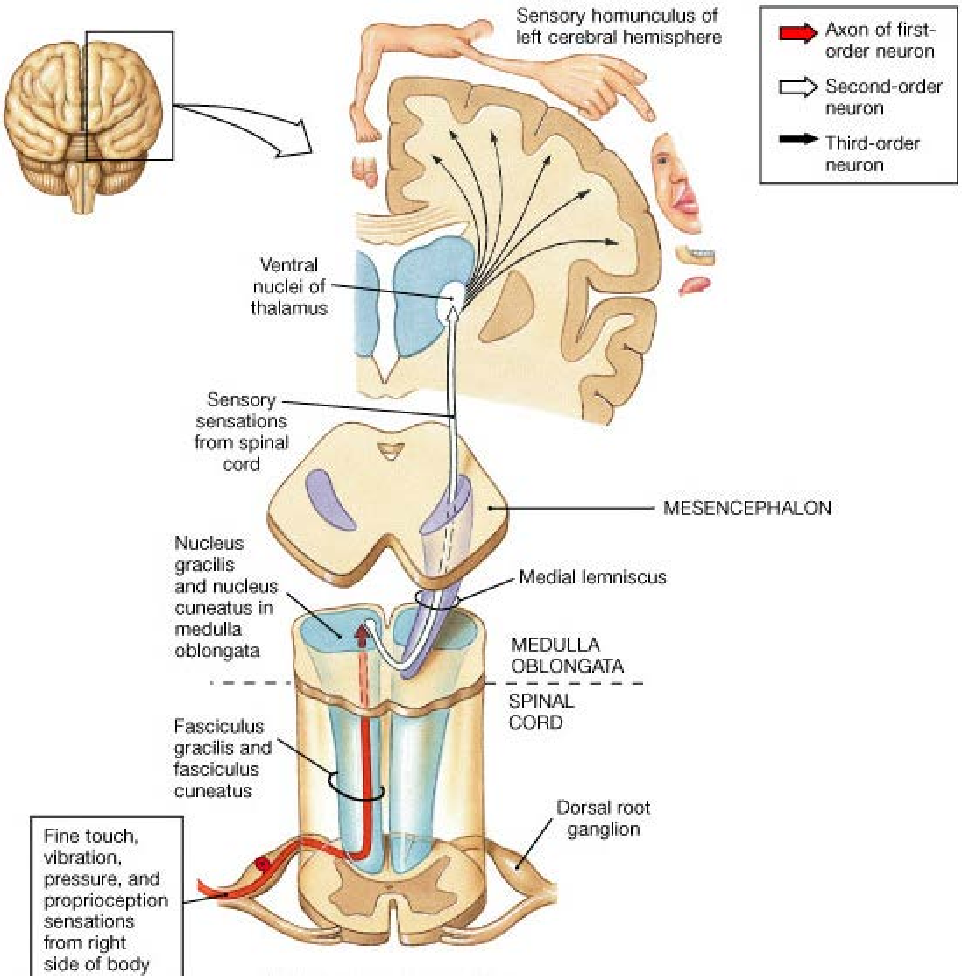

Figure 1.2 Dorsal column-medial lemniscus pathway: first-order neuron enters the spinal cord via the dorsal roots then ascends to medulla level where the second order neuron decussates the midline and ascends to the thalamus where it synapses onto third order neuron that relays afferent signals to the primary somatosensory cortex. Image reprinted from https://anatomy-library.com/img/anatomy-dorsal-column-1.html.

Different areas in primary somatosensory cortex (SI), area 3a, 3b, 1 and 2, receive proprioceptive and tactile input from the body. Area 3a receives proprioceptive input from muscles and joints through the ventral posterior superior nucleus. Area 3b receives tactile input from the skin, which is then sent to area 1 and 2 for further processing. Area 2 also plays a role in perceiving size and shape involved with proprioception. Information from SI is sent directly to M1, SII, and somatosensory association cortices. Brodmann's area 5 integrates proprioceptive and haptic information. Brodmann's area 7 integrates proprioceptive and visual spatial information to facilitate localizing objects relative to the body (Debowy, Ghosh, Ro, & Gardner, 2001; Murray & Mishkin, 1984).

Proprioceptive information is also directly and indirectly conveyed to the cerebellum for unconscious use in postural control, coordination and maintaining muscle tone. The main pathways for upper-limb proprioception include spinocerebellar tracts, which transmit afferent inputs from proprioceptors that innervate the lower cervical and upper lumbar spinal levels (dorsal) and lower lumbar and thoracic spinal cord (ventral). That primarily terminate in two topographic maps in the spinocerebellum (anterior lobe and paramedian lobule). A third proprioceptive pathway is the cuneocerebellar tract, which conveys proprioceptive inputs from the upper-limb. Afferent nerve fibers ascend from the lateral cuneate nucleus and terminate topographically in the cerebellum through the ipsilateral inferior cerebellar peduncle.

1.2.1 Hand and Arm Localization

How well can we use proprioceptive information described above to locate our arm or hand? While vision tends to provide more accurate and precise estimate of hand position (Ernst & Banks, 2002; Jones, Cressman, & Henriques, 2010; Sober & Sabes, 2003) than just proprioception, people are still able to locate their unseen hand with a fair amount of accuracy and precision (in the order of a few centimeters, (Jones, Cressman, & Henriques, 2010)), although this depends partly on the tasks and which part of the “limb’ is being assessed. Behavioural tasks used to measure proprioception (in the absence of vision) required participants to either match the position of one hand or arm to the other, localize one hand using the opposite hand, or estimate hand location relative to a reference marker. In this dissertation, we used two of these methods which we describe in detail below.

One task, which we call “hand localization” or “proprioceptive-guided reaching”, assesses how well people can accurately and precisely locate their hidden hand using their opposite hand, or in some labs, a cursor (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Jones et al., 2010; Jones, Fiehler, & Henriques, 2012; Sarlegna & Sainburg, 2007; Synofzik, Lindner, & Thier, 2008; van Beers, Sittig, & van der Gon, 1998; van Beers, Sittig, & van der Gon, 1999). Here people are usually accurate within several centimeters, but with most producing consistent misestimates contingent on the hand tested, such that the left hand is misestimated as being more left and the right hand as being more right than the real hand location (Haggard, Newman, Blundell, & Andrew, 2000; Jones et al., 2010; Sarlegna & Sainburg, 2007, 2009; van Beers et al., 1998, 1999). Moreover, some studies find that locating the left hand is more precise than the right hand, although this could be due to the precision of the indicating hand, and thus may reflect the precision of the reaching/moving hand and not proprioceptive localization ability per se. Indeed, Jones et al (2012) and Jones & Henriques (2010) found that proprioceptive tasks that didn’t involve proprioceptive-guided reaching (see below for more detail) show no significant differences in precision when estimating the left vs right unseen hand location, and only small differences in precision when proprioceptive-guided reaching was used (note: in their study, the reaching hand was dimly lit to reduce these reaching errors). However, they did continue to find a hand-dependent systematic bias as mentioned above: the left hand was judged to be located more left and the right hand more right (each by 1-3 cm of directional error). The results above suggest that hand proprioception is relatively accurate although with a systematic, lateral, hand-dependent bias, but with little difference in proprioceptive precision between the two hands.

The other main task used in the studies by Jones et al. involves a perceptual judgment task to measure the proprioceptive estimate of hand location (what Jones and we sometimes call proprioceptive estimation). The advantage of this method is that it does not require involving the other hand, possibly for a less confounded estimate of hand proprioception. This perceptual judgment task was originally developed by Cressman and Henriques (2009) and it involves asking participants to estimate their hand position relative to visual and proprioceptive reference markers (without planning a reach). The location of the unseen hand (moved or guided by a robot manipulandum) relative to the reference markers varied from trial to trial, using an adaptive staircase algorithm. Once the hand moved to its final position, the reference marker would appear or sound, and participants indicated whether their hand is to the right or left of the reference marker using two-alternative forced choice responses (the right or left arrow keys on a keyboard). Each reference location was tested across 50 trials, and the responses were fitted by logistic function to get the locations at which participants felt their hand to be aligned with the reference markers (see Figure 2.1 for an illustration). For each logistic function, the bias (a measure of accuracy, the point of 50% probability) and uncertainty (a measure of precision, the difference between the values at which the response probability was 25 and 75%) was calculated.

Jones and Henriques (2010) and Jones et al. (2012) compared this perceptual task with the proprioceptive-guided reaching tasks and found that estimates using this perceptual task were similar to those for proprioceptive-guided reaches, although less accurate than a task where participants merely reproduced the location of the hand (in all tasks, the robot guided the hand into position). As mentioned above, in both proprioceptive-guided reaches and proprioceptive-estimation tasks, the authors found that participants perceived their left and right hands to be biased leftward and rightward, respectively.

In the studies in this dissertation, we used both proprioceptive methods to measure the lateral location of felt hand position before and after adapting the target-hand (and the opposite hand in Chapter 2) to a visuomotor distortion. In Chapter 2 and 3, we used the perceptual tasks while in Chapter 4 we used proprioceptive-guided reaching for reasons described later in this Chapter.

1.3 Reach adaptation

While there are many types of motor learning, in this dissertation we are interested in motor adaptation, which involves modifying a movement that is already well learned, like reaching. Adaptation involves forming a novel, context-dependent remapping between a sensory input and a motor output. The process of motor adaptation can be defined as "an error-reduction process that occurs when systematic errors are introduced in body movements by certain internal or external factors" (Tanaka, 2010).

Under laboratory settings, systematic errors can be introduced by using different perturbations which can be dynamic, like a force field, or kinematic, like false visual feedback of the hand (Wolpert, Diedrichsen, & Flanagan, 2011). In force field experiments, a robotic manipulandum is used to apply forces to a participant's hand. Direction and magnitude of these forces usually depend on the state of the hand (i.e., its position and velocity). The participant's reaches are initially displaced laterally (the hand path is curved) when the force field is applied as they move to the target. However, they quickly adapt their reaches to move directly to the target (straight path) as they do for normal, unperturbed reaches. In visuomotor adaptation training, as I mentioned earlier, participants are asked to reach to one or more targets with a cursor that misrepresents their unseen hand position. That is, during training, a misalignment is introduced between the actual hand movement and the cursor motion (by rotating the path of the cursor either CW or CCW relative to the hand) so that cursor deviates away from the target direction at the beginning of training. By 20 or so reaches (per target, Krakauer et al., 2000) for a small cursor rotation (like 45 degrees), participants learn to redirect their unseen hand movements to get the cursor directly to the target. For both types of perturbations, error or reach deviations are initially quite large, but reduce quite quickly in an exponential manner. That is, improvement is large and fast at the beginning of training, followed by slower improvements of performance until they return to pre-perturbation (baseline) levels.

Following reach training with perturbations, reaches continue to deviate after the perturbation is removed, by making the cursor invisible or by realigning it with the hand. These reach aftereffects provide another measure of reach adaptation. When reach adaptation occurs, participants show reach aftereffects in the opposite direction of the introduced rotation when reaching without a cursor. Reach aftereffects for visuomotor adaptation emerge quickly during training, within a dozen reach-training trials (Ruttle et al., 2016), and after training, are usually around 50% of the introduced distortion in size, regardless of the type (rotated or translated), size or direction of the introduced cursor-misalignment, or whether the cursor is continuously visible during reaches or only shown at the end of the movement (Abeele & Bock, 2001; Criscimagna-Hemminger, Bastian, & Shadmehr, 2003; Krakauer et al., 2000; Salomonczyk, Cressman, & Henriques, 2011). As an example, in their experiments, Cressman and Henriques (2009) trained their participants to reach to visual targets with a visuomotor distortion where the cursor was rotated 30° or laterally-shifted 4-cm. The authors found that regardless of the type of visuomotor distortion (rotated vs. translated), reach adaptation occurred to a similar extent, with reach aftereffects of ~ 18° on average relative to hand starting position. Interestingly, reach aftereffects were found to be robust enough to be retained up to 24 hours following training (Nourouzpour, Salomonczyk, Cressman, & Henriques, 2014). Reach aftereffects are large for open-loop reaches produced to the trained target locations, and decrease in magnitude as the location of novel targets are farther from the trained direction (explained in more details below). Thus, reach aftereffects not only provide measures of adaptation, but also of how this adaptation generalizes.

Most theories of motor learning hold that adaptation is driven by a mismatch between actual and predicted consequences of hand movement (Wolpert et al., 2011) and training with a perturbation leads to updates or modifications in these predictions, which in turn lead to the resulting modifications of the movement. Such predictions are produced every time we make a movement and are based on an efference copy of the outgoing movements. The predictions or simulations are produced by what is conceptually known as a forward internal model. The role of forward model is illustrated in Figure 1.3; it receives a copy of selected motor commands which allows it to predict the motor commands' sensory outcome. Based on this efference copy, a comparison between predicted and actual sensory input of the selected motor command takes place. If there is a mismatch between the two, then the motor command must be adjusted and a new internal model be formed. In motor adaptation studies, reach aftereffects have been proposed to reflect an establishment of a new internal model which is associated with the novel sensorimotor transformation (e.g., Haith & Krakauer, 2013;Wang & Lei, 2015; Wolpert, Ghahramani, & Jordan, 1995). Despite the crucial role that these updates in predictions play in adaptation, it is not clear how much these changes in efference-based estimates of hand position contribute to hand localization when compared with those of purely sensory-based estimates.

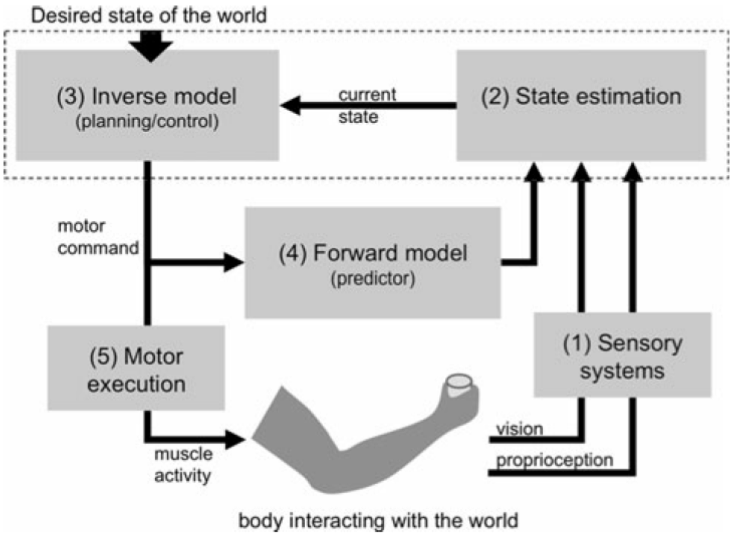

Figure 1.3 Vision and proprioception provide information to estimate the position of the hand and cup location. A motor command is sent to the hand to reach a cup and an efference copy of this motor command is sent to a forward model. Forward model predicts the sensory consequences of the motor command and compares it with the actual sensory feedback (Gowen & Hamilton, 2013)

In visuomotor adaptation training, the sensorimotor or prediction errors described above are not the only errors that can drive adaptation. Our lab has shown that even cross-sensory exposure training, where there are no volitional movements are performed throughout training, leads to reach adaptation (Cressman & Henriques, 2010). In their study, Cressman & Henriques (2010) showed that participants produce reach aftereffects even without any volitional movements and therefore no efference-based predictions. During training, the participant's hand was passively moved and gradually rotated while the visual feedback always indicated that the cursor (which represents hand movement) was heading to the target with no visual reach errors. They refer to this type of training as cross-sensory exposure training, because it involves exposing participants only to the visual-proprioceptive discrepancy. After training, participants adapted their subsequent open-loop reaches in the direction of the introduced visual feedback, similar to reach aftereffects observed following classical visuomotor training albeit smaller in size. This suggests that training with visual-proprioceptive discrepancy influences reach adaptation.

In classical visuomotor adaption training tasks, participants are exposed to two types of error signals; a) sensorimotor or prediction error signal, generally known as an error-based signals (Haith & Krakauer, 2013), b) visual-proprioceptive discrepancy signal, i.e., mismatch between the seen and felt hand position. If prediction error is the driving force for reach adaptation, then participants should not adapt their reaches if they do not experience prediction errors during training. However, this is not the case as mentioned above in Cressman and Henriuques (2010) and in other studies where it is shown that cross-sensory exposure training leads to motor changes, even though no volitional movements are performed throughout training (Cameron et al., 2012; Sakamoto & Kondo, 2015). These findings suggest that two different types of error signals drive reach adaptation and both need to be taken into account when interpreting empirical results.

1.4 Proprioceptive recalibration

There is emerging evidence from behavioral studies that motor adaptation involves not only changes in movement but also perceptual changes in estimates of hand position and motion. These perceptual changes have been shown to occur after adaptation to various perturbations including visuomotor adaptation, prism adaptation, and force-field adaptation (for a review, (Ostry & Gribble, 2016)). Using visuomotor adaptation training paradigms, our lab has shown that, in addition to motor changes, visuomotor adaptation training leads to changes in the felt hand position toward the previously introduced visual feedback; a process we call proprioceptive recalibration (e.g., Cressman & Henriques, 2011; Cressman & Henriques, 2009). In their experiments, Cressman and Henriques (2009) measured this proprioceptive change following visuomotor rotation and lateral translation training using a perceptual testing task (proprioceptive estimation task, introduced above). Specifically, they used a 30° rotation and a 4-cm shift in the training tasks (the 4-cm shift corresponded to the average horizontal shift achieved across the workspace as 30° rotation). They measured people's estimates of their unseen hand's position, both before and following training. They did so using one of the methods described in Section 1.2, in brief, by having participants make a forced-choice judgment (left or right) of the position of their unseen hand relative to a visual or proprioceptive (a non-visual, i.e., body midline) reference marker. The authors were able to find that regardless of the introduced visuomotor distortion (rotated vs. translated) and how the hand was moved to its tested location (either displaced by the robot, passive displacement, or constrained by the robot, active displacement), proprioception was recalibrated to a similar extent in all conditions. The size of this proprioceptive recalibration was 6° following rotation training and 0.8 cm following lateral translation training. The magnitude of proprioceptive recalibration was found to be more than one third of the size of aftereffects in several studies (for a review, Henriques & Cressman, 2012). This recalibration magnitude found to increase proportionally if the introduced rotation increases. For example, Salomonczyk et al. (2011) exposed participants to visual feedback rotated by a 30°, 50°, 70°, as the distortion increased the resulting hand proprioceptive recalibration also increased. Nonetheless, the shift was proportional (about 20%) to the magnitude of the introduced rotation. Moreover, following visuomotor adaptation proprioceptive recalibration was found to be similar in extent in older healthy adults and young adults, although older adults had higher uncertainty (Cressman, Salomonczyk, & Henriques, 2010; for a complete review see, Henriques & Cressman, 2012). These findings show that visuomotor adaptation training induces a robust shift in felt hand position in addition to motor changes.

In accordance with our findings, force field adaption studies report a similar proprioceptive shift following training. For example, Ostry and colleagues (2010) examined changes in felt hand motion following force field adaptation training by having participants estimate the direction by which their hand deviates along a specified path. They found a significant change in felt hand motion to the opposite direction of the introduced force field. Additionally, this shift was durable and lasted for 24 hours. It is noteworthy that, in force field adaptation, there is no mismatch between felt hand motion and visual feedback of the hand, but, motor adaptation is accompanied by felt hand position changes. Moreover, following prism adaptation both vision and felt arm position were found to be spatially shifted. Harris (1963) interpreted the shift in open-loop or straight ahead pointing as proprioceptive realignment. Of note, when assessing hand proprioception using open-loop reaching or pointing any proprioceptive shifts might be confounded by motor effects. However, this fact does not suggest that a proprioceptive shift does not occur following prism adaptation training. In another prism adaptation study, participants were able to retain this proprioceptive shift up to 7 days following training (Hatada, Rossetti, & Miall, 2006). Combined these findings suggest that a shift in felt estimates of hand position and motion occurs as a result of adaption training.

Proprioceptive recalibration has important implications in movement control and learning, given that any changes in estimating hand position will affect the integration process of visual and proprioceptive information that the brain uses in order to plan and execute an accurate reach towards a given target. Studying proprioceptive recalibration will help in understanding the contributions of sensory plasticity in motor learning. The first two studies in this dissertation were designed to examining the extent by which motor changes and changes in hand proprioception generalize between hands and across the work space.

1.5 Generalization of reach adaptation

Learning is not only restricted to the training context but can partly transfer, or generalize, to other similar contexts. The extent and pattern of generalization can provide insights into how the brain interprets performance errors in order to adapt. To answer some questions such as what mechanisms underlie generalization of motor adaptation and how neural information is stored and updated, several studies have investigated whether and how motor adaptation transfers (1) between limbs and (2) across the workspace.

1.5.1 Intermanual transfer

Intermanual transfer has been measured using a variety of learning tasks such as finger tapping (Laszlo, Baguley, & Bairstow, 1970), reaching with prisms (Taub & Goldberg, 1973), figure drawing (Thut et al., 1996), grasping objects (Chang, Flanagan, & Goodale, 2007), and reaching in force fields (Dizio & Lackner, 1995; Wang & Sainburg, 2003). Intermanual transfer for motor adaptation has been tested by asking participants, following visuomotor rotation training, to reach using the untrained hand to the trained targets with perturbed feedback of the hand or without visual feedback of the hand (Sainburg & Wang, 2002; Salomonczyk et al., 2012). Accordingly, any observed improvements or changes when subjects reach to the trained targets with the untrained hand, can be attributed to motor adaptation having been transferred from the trained to the untrained hand. For example, in a case where someone adapts the left hand-reach in response to a rotated cursor, transfer would mean that when the right-hand then reaches with the same rotated cursor, it should learn faster and perhaps show smaller initial errors compared to a group who did not train with their left hand prior to reaching with their right hand. Previous intermanual transfer studies have found different results; some suggest that transfer partially occurs (some benefits to the second hand) and others suggest that it does not occur at all. With regard to the direction of transfer, some studies have documented asymmetric transfer from the non-dominant to the dominant hand (Wang & Sainburg, 2004), while others have found that motor changes transfer from the dominant to the non-dominant hand (Balitsky Thompson, & Henriques, 2010; Taylor, Wojaczynski, & Ivry, 2011). Other studies have shown that intermanual transfer of specific variables occurs in both directions, that is, final-position information transfers from the dominant to non-dominant hand, and direction information transfers from the non-dominant to dominant hand (Sainburg & Wang, 2002; Wang & Sainburg, 2003). Of note in all the above mentioned studies, the amount of observed intermanual transfer was proportional to the total amount of adaptation in the trained hand.

Theoretically, three different models have been proposed as an explanation to these reports: the “callosal access model” which argues that when training with one hand, regardless of the hand used, a single memory is stored in the dominant hand hemisphere, so that the dominant hand benefits from the non-dominant hand training (Taylor & Heilman, 1980). Second, the “cross-activation model” posits that only training with the dominant hand stores a weaker copy of memory in the non-dominant hand hemisphere, which influences the non-dominant hand performance; finally the “modified access model”, which posits that information stored during learning with either arm controller can subsequently be accessed by its contralateral homolog (Sainburg & Wang, 2002).

Previous work in our lab has found asymmetrical intermanual transfer of motor adaptation following reach training with rotated visual feedback. Specifically, two groups of subjects performed a reaching task using one hand, each with two different viewing conditions (i.e., a 45° and 75° CCW rotated cursor or rotated view of their actual hand). After adaptation, subjects reached with the opposite hand to the same targets (under the same viewing conditions). Equivalent amounts of intermanual transfer were found across the different magnitudes of rotation. However, asymmetric transfer from the dominant to non-dominant hand was observed (Balitsky, Thompson, & Henriques, 2010). The authors have suggested that these results are due to symmetrically lateralized limb control but asymmetrical spatial mapping, where the right limb is represented in both hemispheres, while the left limb is represented only in the right hemisphere. However, more recently, another more computational explanation has been offered by Berniker and Kording (2008) where generalization is based on how the brain interprets the source of the observed error. If the CNS attributes error in reaches to some impairment or changes of limb properties, then using the same arm, the adapted reaching movements should apply to different locations along the workspace, but not to the opposite to arm. But to the extent that some of the error is attributed to external sources or the environment, (like a defective hammer), then generalization to that extent should transfer to the opposite arm. Their model also explains asymmetries in transfer between the two arms, such that reach errors by the non-dominant arm will be assigned mainly to the arm and not the environment, which may result in no or little transfer of learning to the opposite dominant arm.

1.5.2 Workspace-generalization

Generalization designs have been widely investigated in visuomotor adaptation studies (e.g., Ghahramani, Wolpert, & Jordan, 1996; Krakauer et al., 2000). The patterns of generalization across workspace have provided insight about how goal-directed reaches are computed and updated during adaptation (Krakauer et al., 2000). Typically, the way motor adaptation generalizes across the workspace has been tested by asking subjects to reach, following visuomotor training, to untrained directions or distances from different or same starting locations (e.g., Krakauer et al., 2000; Wu & Smith, 2013). Findings have shown that adaptation to a single target leads to a narrow or local generalization pattern across novel-untrained directions such that generalization is found to be greatest at novel targets near the training target direction and decays at novel targets further away from it. That is, generalization across different movement directions tends to be "local"; largest near the trained direction. However, the pattern of generalization across novel-untrained distances have shown to be broad such that similar amount of motor adaptation is observed at novel targets in the same direction but at different distances (relative to training target). In one seminal paper on this topic, Krakauer et al. (2000) found that reach training to a single target with a cursor rotated 30° CW resulted in the generalization of ~80% of motor adaptation to novel targets that deviated by 22.5° from the trained direction, and only ~25% to novel targets that deviated by 45°. However, subjects successfully adapted their reaches to a similar extent when they reached to novel targets at different distances (2.4, 4.8, and 9.6 cm) from the starting position, but in the same direction as the trained target. The same generalization patterns for motor adaptation have been documented by several other studies (e.g., Neva & Henriques, 2013; Shabbott & Sainburg, 2010; Wu & Smith, 2013). Paz et al. (2003) showed that monkeys adapted their reaches and showed a similar "local" generalization curve as humans. The authors recorded the activity of neurons in M1 while monkeys reached to trained and untrained directions and found no change in activity when reaches were made to directions more than 30° right or left of the trained direction. These findings show evidence for a strong relation between the patterns of generalization for visuomotor adaptation, and the properties of neurons in the motor system, i.e., their directional tuning. Given that the learning-induced changes tend to be direction-specific, it may not be surprising that movements made in the same direction but at different amplitude would still benefit from learning and hence explain why generalization of adaptation to different movement amplitude is not so narrow. This is consistent with the interpretation by Goodbody and Wolpert

(1998), they 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.

1.6 Generalization of proprioceptive recalibration

As introduced above, several visuomotor adaptation studies have focused on examining how reach adaptation generalizes across limbs, and different directions or distances in the workspace. However, very few studies have explored how sensory changes generalize with adaptation. As mentioned previously, our lab and others have shown that visuomotor adaptation leads not only to motor changes, but also to proprioceptive recalibration (e.g., Cressman & Henriques, 2011; Cressman & Henriques, 2009). A recent study in our lab has shown that the generalization patterns of proprioceptive recalibration and reach adaptation are different. Specifically, Cressman and Henriques (2015) showed that independent of reach adaptation, which showed a similar localized generalization pattern as seen in Krakauer et al. (2000), proprioceptive recalibration generalized across novel directions. It is yet unclear, however, whether proprioceptive recalibration will broadly generalize, like motor adaptation, to different distances in the workspace. Moreover, intermanual transfer of proprioceptive recalibration has not been investigated previously. In Chapter two we examined how proprioceptive recalibration transfers between the two hands.

Indeed, proprioceptive recalibration is of great interest, given that any changes in estimating hand position will affect the integration process of visual and proprioceptive information that the brain uses in order to plan and execute an accurate reach towards a given target. Studying proprioceptive recalibration can help in understanding the contributions of sensory plasticity in motor learning. Furthermore, it can help explain some observed results in motor learning literature, such as the incomplete transfer of motor adaptation to the untrained hand. If visuomotor adaptation with one hand does not lead to changes in the opposite hand's proprioception, then we can conclude that proprioceptive recalibration, unlike motor adaptation, is specific to the exposed hand because both processes occur after visuomotor training. Differences between the way sensory and motor changes generalize may suggest that the two processes are somehow independent and may arise from independent error signals. The first goal in this dissertation is to examine the extent by which the motor changes and changes in hand proprioception transfer to the opposite hand.

1.7 Objectives

This dissertation specifically examines the characteristics of reach adaptation and proprioceptive recalibration. Chapter two examines if proprioceptive recalibration transfers intermanually following training with translated visual feedback of the hand and if this transfer is symmetrical between hands. Chapter three examines how proprioceptive changes generalize to different distances following visuomotor adaptation, and investigates the correlation between motor and sensory changes. Chapter four examines how sensory prediction and proprioception contribute to reach aftereffects and changes in hand localization following adaptation, and examines the pattern of generalization across different directions for reach adaptation and proprioceptive recalibration following cross-sensory exposure training. In each Chapter, the rationale, hypotheses, methods, results and discussion of findings will be articulated in detail.

CHAPTER TWO

INTERMANUAL TRANSFER AND PROPRIOCEPTIVE RECALIBRATION FOLLOWING TRAINING WITH TRANSLATED VISUAL FEEDBACK OF THE HAND

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Experimental Brain Research

2.1 Abstract

Reaching with visual feedback that is misaligned with respect to the actual hand's location leads to changes in reach trajectories (i.e., visuomotor adaptation). Previous studies have also demonstrated that when training to reach with misaligned visual feedback of the hand, the opposite hand also partially adapts, providing evidence of intermanual transfer. Moreover, our lab has shown that visuomotor adaptation to a misaligned hand cursor, either translated or rotated relative to the hand, also leads to changes in felt hand position (what we call proprioceptive recalibration), such that subjects' estimate of felt hand position relative to both visual and non-visual reference markers (e.g., body midline), shifts in the direction of the visuomotor distortion. In the present study, we first determined the extent that motor adaptation to a translated cursor leads to transfer to the opposite hand, and whether this transfer differs across the dominant and non-dominant hands. Second, we looked to establish whether changes in hand proprioception that occur with the trained hand following adaptation also transfer to the untrained hand. We found intermanual motor transfer to the left untrained (non-dominant) hand after subjects trained their right (dominant) hand to reach with translated visual feedback of their hand. Motor transfer from the left trained to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike visuomotor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

2.2 Introduction

Moving the hand while its visual feedback is distorted leads to a mismatch of vision and action that results in sensorimotor remapping and adaptation. For example, when subjects first reach to a target with distorted visual feedback (e.g., a cursor that is rotated or translated relative to the hand's actual motion), the cursor-reaches are initially deviated but are then gradually adjusted or adapted across trials so that later reaches bring the cursor more directly to the target (Krakauer et al. 1999; Sainburg and Wang 2002; Simani et al. 2007). This visuomotor adaptation has also been shown to transfer across arms, which is referred to as intermanual transfer. In such cases, learning with one hand facilitates subsequent performance with the opposite, untrained hand. Intermanual transfer has been observed in such tasks as drawing (Thut et al. 1996), grasping (Chang et al. 2008), pointing and tracking (Abeele and Bock 2003). More importantly for the current study, intermanual transfer also occurs after adapting reaching movements to displacing prisms (Hamilton and Bossom 1964), force perturbations (Dizio and Lackner 1995), mirror-reversed visual feedback (Dionne and Henriques 2008) and rotated visual feedback of the hand or cursor (Wang and Sainburg 2003; 2004; 2006; 2007; Balitsky, Thompson, & Henriques 2010).Typically intermanual transfer of adaptation to these various perturbations is assessed by testing the untrained hand to the same perturbation that the trained hand has adapted to. Transfer is said to occur when initial errors in response to the perturbation are smaller and/or the learning rate is faster for the untrained hand following training of the opposite hand compared to when there is no initial adaptation in the opposite hand.

The pattern of intermanual transfer is not necessary the same across the two hands. In a series of experiments by Sainburg and Wang (2002; 2003), they found that when subjects adapted one of their hands to a rotated cursor (visuomotor rotation), the transfer of this learning to the opposite arm was asymmetric, in that the size and types of intermanual transfer depended on the hand trained. Specifically, they found that final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. They proposed that this intermanual transfer pattern reflects basic differences in or specialization of the two arm controllers, such that the initial direction information transferred to the right arm controller from the non-dominant arm. However, the endpoint configuration of the limb, but not the initial direction, transferred to the left arm controller from the dominant arm. In contrast, Balitsky, Thompson, and Henriques (2010) found intermanual transfer occurred only from the dominant right hand to the left hand, but not from the non-dominant left hand to the right hand, and this was the case when subjects adapted to a rotated cursor or to a rotated video image of the hands (based on angular deviations at peak velocity when the untrained hand reached with the same altered visual feedback). Other motor adaptation studies where subjects adapted to velocity-dependent force fields (Criscimagna-Hemminger et al., 2003), also measuring deviations at peak velocity during training with the previously untrained hand) and displacing prisms (Redding and Wallace 2008), measuring reach endpoint deviations of the opposite arm without the prisms; e.g., aftereffects), have shown a similar asymmetry, training with the dominant hand leads to facilitation with the non-dominant hand.

In the current study, our first goal was to investigate the nature and extent of intermanual transfer after adaptation to a translated cursor. We used a translated cursor (i.e., the cursor appeared rightward of the actual position of the hand and it moved parallel with the hand) as our perturbation rather than the usual rotated cursor (i.e., while the subject moves his/her hand forward, the cursor heads off on a directional angle relative to the hand) since previous results from our lab suggest that proportional changes in reaches measured by the resulting aftereffects (relative to the magnitude of the distortion), are greater after adaptation to a translated cursor than to a rotated cursor (Cressman and Henriques 2009). In fact, previous studies by Ghahramani et al. (1996) and Vetter et al. (1999) suggest that adapting to a shifted or translated cursor may also lead to greater generalization across the workspace compared to adapting to a rotated cursor (Krakauer et al. 2000). This difference in both generalization and size of aftereffects following adaptation to a translated cursor compared to a rotated cursor makes sense in that the translated feedback of the hand resembles the kind of visual perturbation one may experience in everyday life, like refracted light from submerging our hand in water, or using a tool that extends or shifts our end-effector. Even a computer mouse resembles a translated shift of the hand more than a rotated shift. In contrast, a rotation perturbation is something we would not experience in everyday life and hence may be more difficult to adapt to. Thus, we used a translated cursor for adapting the hand to provide the greatest possibility of observing intermanual transfer, which is a type of generalization, and one that has not been studied before following translated-cursor adaptation. We assessed the extent and pattern of this intermanual transfer of reach adaptation by using a no-cursor (open-loop) reaching task to measure aftereffects of both the trained and untrained hand. We also examined whether this transfer differed across the dominant and non-dominant hands. Given the previous studies mentioned above and those in our lab (Balitsky Thompson and Henriques 2010; Salomonczyk et al. 2010) demonstrating that intermanual transfer occurs asymmetrically depending upon the trained hand, in the current study, we hypothesized a similar asymmetry after training with a translated cursor.

In addition to examining intermanual transfer of reach adaptation, we investigated whether changes in felt hand position (i.e., proprioceptive recalibration) also transferred between limbs (what we will call intermanual sensory transfer). Recent studies have shown that visuomotor adaptation leads not only to changes in trajectory of the trained hand, but that the felt position of the hand is also modified (Cressman and Henriques 2009; 2010; Cressman et al. 2010; Ostry et al. 2010; Cressman and Henriques 2011; Salomonczyk et al. 2011). In our own lab, we have found that adapting to either a rotated or translated cursor leads to changes in hand proprioception, such that people perceived their unseen hand as being shifted in the direction of the visual distortion (Cressman and Henriques 2009; 2010). To determine changes in felt hand position we have subjects estimate the location of their unseen hand relative to a visual or proprioceptive (body midline) reference marker both before and following visuomotor adaptation (Cressman and Henriques 2009; 2010). To date, it has been shown that this proprioceptive recalibration is robust in that it occurs under various task constraints (i.e., adapting to a visuomotor distortion or velocity dependent force field) (Cressman and Henriques 2009; 2010; Ostry et al. 2010), regardless of how the hand is displaced during this proprioceptive estimation task (passive arm displacement vs. active reaching movements) (Cressman and Henriques 2009; 2010), the modality of the reference markers (visual vs. proprioceptive) and the age of the patients (young vs. older adults) (Cressman and Henriques 2009; 2010).

Previous studies examining proprioceptive recalibration have focused on assessing shifts in felt right-hand position following motor learning of the right arm in right-handed individuals. It is currently unclear whether, like motor adaptation, such sensory changes transfer to the opposite untrained hand as well. Thus, after establishing the nature and extent of intermanual motor transfer, the second goal of this study was to test whether proprioceptive recalibration transfers from the trained (right or left) hand to the untrained (left or right) hand following adaptation to a visuomotor distortion, and whether this transfer occurs asymmetrically depending upon the hand trained.

2.3 Methods

2.3.1 Subjects

In total, 35 right-handed subjects (mean age=22.9, SD=5.62, 11 male) were randomly assigned to either the left hand (n= 17) or right hand (n= 18) training groups. 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 towards an undergraduate psychology course.

2.3.2 General experimental setup

The experimental setup is illustrated in Fig. 2.1A. Subjects were seated in a chair and the height of the chair was adjusted to ensure that they could easily see all of the targets presented on a reflected screen and comfortably reach to target locations. Subjects were asked to hold on (either with their right or left hand) to the vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA) 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 72Hz) 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 own hand was blocked by the reflective surface, as well as a black cloth draped over their shoulders.

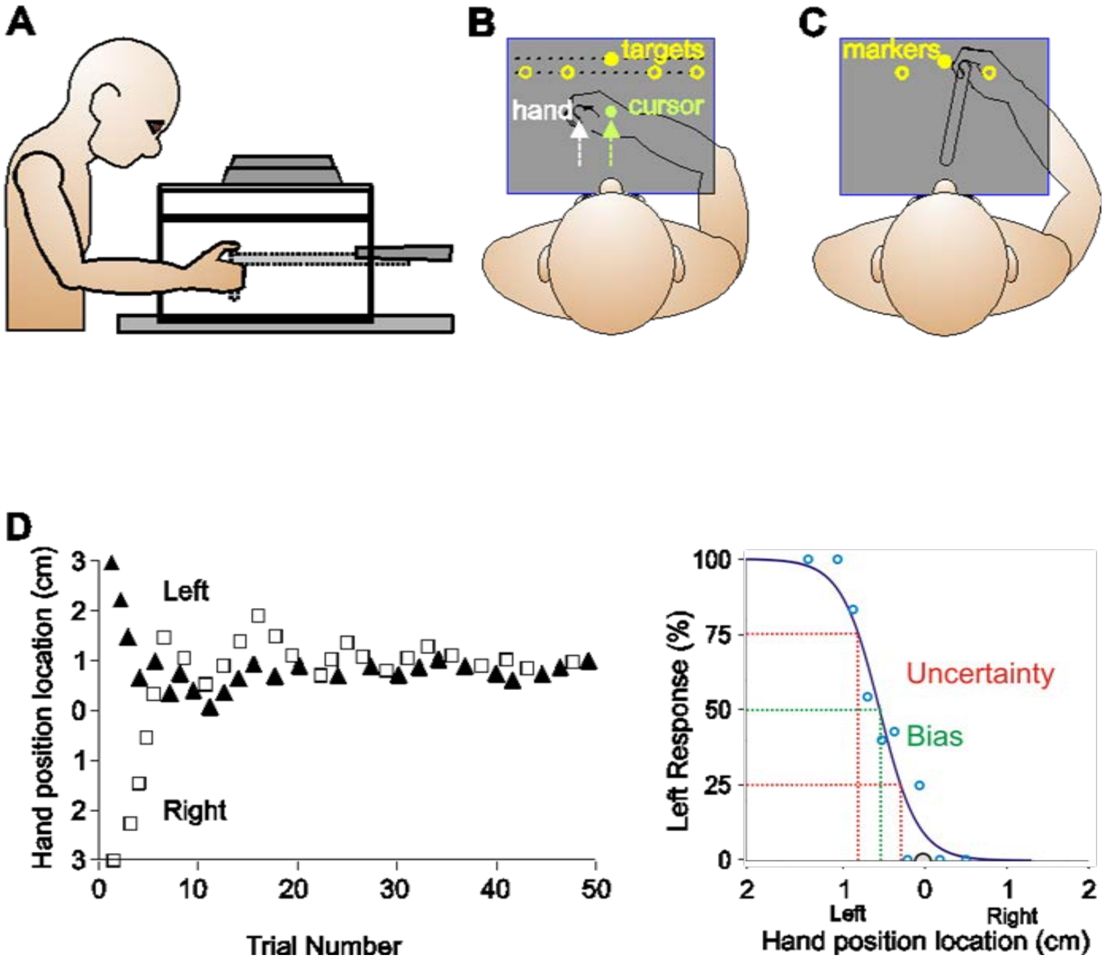

Figure 2.1 Experimental setup and design. **A** Side view of the experimental setup. **B** Top view of experimental setup visible to subjects in the reaching tasks. The center home position was represented by a 1-cm *green circle* and was located about 20 cm in front of subjects' chests, aligned with the body midline, this position was not illuminated, and visual feedback was provided only when the hand had travelled 4 cm outwards from the home position. Five targets were located along 2 lines; one target was located 10 cm directly in front of the home position and was represented by a *yellow circle* 1 cm in diameter. Four additional targets were located 5 and 7.5 cm to the left and right of the center target, 8.66 cm in front of the home position. The visuomotor distortion was introduced gradually until the cursor was translated 4 cm rightward with respect to the hand. This shift ensured that the *green cursor* (representing the hand) appeared to come from a central position. **C** Top view of experimental surface visible to subjects in the proprioceptive estimates tasks. One reference marker was located 10 cm directly in front of the home position and was represented visually by a *yellow disk*, 1 cm in diameter or proprioceptively (body midline). Two additional reference markers were located 5 cm to the left and right of the center reference marker, 8.66 cm in front of the home position. **D** Staircase and uncertainty range for the data of one subject for one reference marker. For the left panel, the staircase depicted with triangles illustrated the adjusted hand position across trials for the staircase starting at 3 cm leftward of the reference marker, while the squares illustrate the staircase starting 3 cm rightward. In the right panel, *circles* represent the mean percentage of responses by which the subject reported the hand was left of the visual reference marker across various hand locations. The *green line* intersecting the *x*-axis shows the bias (the

point at which the probability of responding left was 50 %), while the *red lines* depict the uncertainty range (the difference between the values at which the probability of responding left was 25 and 75 %)

2.3.3 Procedure

The experiment consisted of 2 test sessions run on 2 separate days. Each test session consisted of 8 tasks (see Fig 2.2). The first session had subjects reach to visual targets, after training to reach with a cursor that was *aligned* with either their right or left hand's position. The second session, however, had subjects complete the same reach trials after the right or left hand reached with a cursor that was *misaligned* from their hand's position. The misaligned cursor was translated 4 cm to the right of their actual hand position, with this translation being introduced gradually (as described below).

2.3.3.1 Aligned reach training task:

The first testing session included aligned reach training (boxes 1 and 5 in Fig 2.2), where subjects were asked to reach to one of five targets with their right or left hand, hidden from view, but represented by a cursor (green circle, 1.4 cm in diameter, Fig 2.1B) located above their thumb. In front of the home position, which was approximately 20 cm in front of subjects' chests, there were 5 reach targets represented by 1 cm diameter yellow circles, located along two lines, 8.66 or 10 cm above the home position. One reach target was located 10 cm directly in front of the home position. Four additional visual reach targets were located 5 and 7.5 cm to the left and right of the center reach target, 8.66 cm in front of the home position. The reach trial was considered complete when the center of the cursor had moved to within 0.5 cm of the target's center. At that point, both the target and cursor were removed 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 trials, 12 trials for each target.

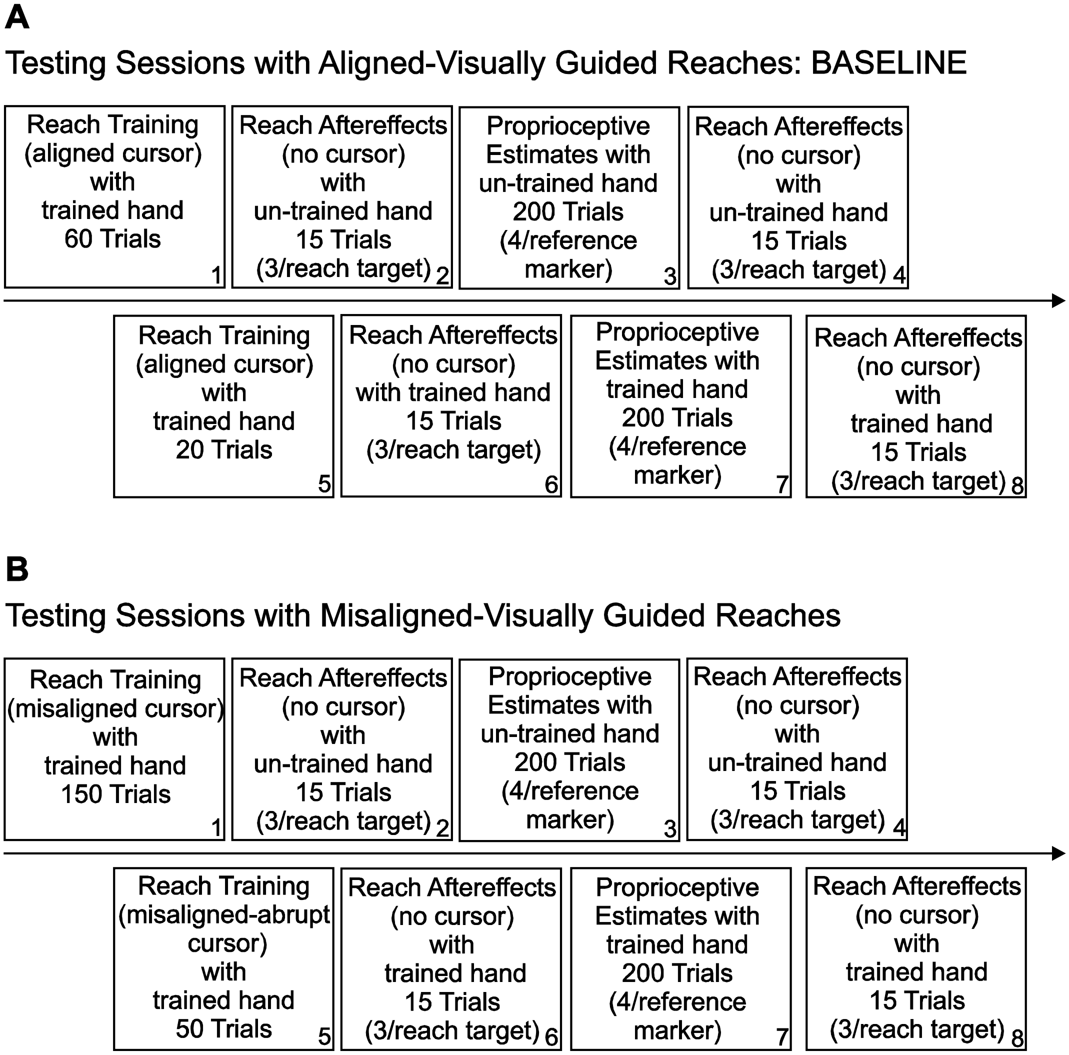

Figure 2.2 Breakdown of the testing sessions within each experiment. **A** Testing session(s) which provided baseline measures of performance. Subjects began their first testing session by reaching to visual targets with their right or left hand (trained hand) while a cursor accurately represented the location of their unseen hand (*box* 1). After completing 60 visually guided reach trials, subjects then reached with their opposite hand (untrained hand) to each of the 5 reach targets, three trials each, without a cursor to assess visuomotor adaptation (reach aftereffect trials, *box* 2). Subjects then completed 200 proprioceptive estimates trials with their untrained hand (*box* 3). After completing the proprioceptive estimate task, subjects completed 15 reaches without the cursor, 3 reaches to all 5 target positions with their untrained hand (*box* 4). Then, they completed a short aligned training task with the trained hand (*box* 5). After completing 20 visually guided reach trials, subjects (trained hand) completed 15 reach trials without the cursor using the trained hand (*box* 6). Subjects then completed 200 proprioceptive estimates trials with their trained hand (*box* 7). The end of this session consisted of 15 reach trials, without a cursor, using their trained hand (*box* 8). **b** In the testing session(s) completed on the second day of the experiment, subjects performed 150 visually guided reaching trials using their right or left trained hand in which the 4-cm rightwards distortion was introduced gradually (*box* 1). Subjects then performed the same tasks as on the first day with their untrained hand (*boxes* 2, 3 and 4). After completing these tasks, subjects completed 50 visually guided reaching trials with the trained hand with a

misaligned cursor, which was presented abruptly (*box* 5). Then, subjects did the same tasks as done on the first day with their trained hand (*boxes* 6, 7 and 8)

2.3.3.2 No cursor reaching task: reach errors assessment

Immediately after the aligned reach training task, subjects reached to the same five targets 3 times each without a cursor (box 2 in Fig 2.2). 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 five reach targets would appear. Subjects were asked to reach to the visible target (as in the previous task) with the robot handle without the cursor or any visual feedback of their hand. Once the reach movement was complete (final position was held for 250 ms), the target and the home position disappeared. This cued subjects to actively move their unseen hand back to the home position along a constrained path to begin the next trial. This task was completed twice by each hand, first by the untrained hand from the previous training task (boxes 2 and 4 in Fig 2.2) and then by the trained hand (boxes 6 and 8 in Fig 2.2).

2.3.3.3 Proprioceptive estimates task: sense of felt hand position assessment

In the proprioceptive estimate trials (boxes 3 and 7 in Fig 2.2), we determined the position at which subjects perceived their unseen hand was aligned with the four reference markers. A proprioceptive estimate trial began with subjects grasping the robot manipulandum that was positioned at the home position. Subjects were then to actively push the robot handle outwards along a constrained path to a location somewhere along the dotted line shown in Fig. 1B (dotted line is for illustration purposes only and was not visible to the subjects). Once the hand arrived at its final position, one of the three visual reference markers 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 if their hand was to the right or left of the reference marker (using the right or left arrow keys on a keyboard). The four reference markers for the proprioceptive estimates were located along two lines, 8.66 or 10 cm, in front of the home position (yellow circles, Fig 2.1C). One reference marker was located 10 cm directly in front of the home position and was represented visually (yellow disk, 1 cm in diameter) or proprioceptively. This proprioceptive reference marker position was based on an internal representation of body midline. Two additional visual reference markers were located 5 cm to the left and right of the center target, 8.66 cm in front of the home position. There were 200 trials in this task, 50 trials for each target.

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 (illustrated as triangles and squares in the left panel of Fig 1D), that were adjusted independently and randomly interleaved. Each staircase began such that the hand was 3 cm to the left or right of the reference marker. The position of the hand was then adjusted over trials depending on subjects' 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 (Fig 2.1D).

2.3.3.4 Misaligned reach training task:

The tasks for the second testing session were similar to the first except for the reaching training tasks, which involved a misaligned cursor (Boxes 1 and 5 in Fig 2.2B). In this misaligned reach training task, the cursor was translated 4 cm rightwards with respect to the actual hand location in the reach training task. To ensure that subjects were unaware of the visuomotor distortion, this shift in cursor position was introduced gradually over the first 41 reach training trials, and thus continue at this maximum cursor translation for the remaining 109 trials for this task (box 1 in Fig 2.2B) and for the subsequent task (box 5 in Fig 2.2B). This was done by shifting the start position of the hand 1.0 mm leftward every trial until it reached 4 cm. The same targets and cursor were used as those in the aligned reach training tasks. For the gradual translation task there were 150 trials, 30 trials for each target. And for the abrupt translation task there were 50 trials, 10 trials for each target. These tasks were completed by the trained hand in either the left or right hand training group.

2.3.4 Data analysis

2.3.4.1 Visuomotor adaptation

Directional deviations of the hand made during reaching trials without visual feedback were analyzed to assess motor adaptation. Since the cursor was shifted horizontally (to the right of actual hand position), we were only interested in errors in this horizontal direction. Reaching endpoint errors were defined as the horizontal difference between a movement vector (from the home position to reach endpoint) and reference vector (from the home position to the target). Reach errors at peak velocity were defined as the horizontal difference between a movement vector joining the home position and the position of the hand at peak velocity and the reference vector. Both of these errors, which we will refer as aftereffects (i.e., baseline values subtracted from adaptation results), were analyzed to determine if subjects adapted their reaches to the targets after aiming with a translated cursor, and if there were any changes in reach adaptation following the proprioceptive estimate trials. To compare the transfer of aftereffects following training with translated cursor feedback from the trained to the untrained hand 2 Group (right hand trained vs. left hand trained) x 2 Training condition (aligned vs. translated cursor) x 2 Hand used (trained vs. untrained) x 2 Time (following reach training trials vs. following proprioceptive estimate trials) mixed ANOVAs were performed on reaching endpoints and reach errors at peak velocity. To assess intermanual transfer, we specifically looked at the difference between these no-cursor reaches following training with the aligned versus translated cursor in the untrained hand and also compared this to the differences for the trained hand. Hand used, Training condition and Time were treated as within-group variables while Group was treated as a between-group variable. Additionally, due to our study goals, pairwise comparisons were conducted across three main factors (Group, Training, Hand used).

Finally, we assessed the extent of intermanual transfer using an independent t-test to compare the aftereffects (to reduce factors in the analysis we subtracted no-cursor reach errors on Day 1 (baseline) from those on Day 2, so that our new dependent variable was a difference in errors) of the trained and untrained hand for each hand; i.e., trained left hand (from the Left hand group) vs. untrained left hand (from the Right hand group), and trained right hand (from the Right hand group) vs. untrained right hand (from the Left hand group).

2.3.4.2 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, as illustrated in the right panel in Fig 2.1D. From this logistic function we calculated the bias (the point at which the probability of responding left was 50%, shown in green) and uncertainty (the difference between the values at which the probability of responding left was 25% and 75%, shown as blue lines). The bias value is a measure of subjects' accuracy of proprioceptive sense of hand position, while the magnitude of the uncertainty range defines its precision (Cressman and Henriques 2009; Cressman et al. 2010).

Proprioceptive recalibration was assessed by comparing the proprioceptive biases or estimates of hand position after training with a translated cursor with those following an aligned cursor (baseline), not only for the trained hand, but also for the untrained hand, so that we could test for intermanual sensory transfer. To do this, we ran a 2 Group (right hand training vs. left hand training) x 2 Hand used (trained vs. untrained) x 2 Training condition (aligned vs. translated cursor) x 4 Marker location (5 cm to the right vs. 5 cm to the left vs. middle visual vs. middle proprioceptive) mixed ANOVA on the proprioceptive estimates or biases. A similar mixed ANOVA was also run to compare the uncertainty values. Again, due to our interest in examining whether the intermanual transfer differs across hands, we followed these ANOVAs with pre-planned comparisons.

All ANOVA results are reported with Greenhouse–Geisser corrected P values. Differences with a probability of 0.05 were considered to be significant. A Bonferroni correction was applied to all preplanned pairwise comparisons.

2.4 Results

2.4.1 Visuomotor adaptation

Figure 2.3 depicts mean reaching endpoint errors (aftereffects) for (A) the left and right trained hands, and (B) the right and left untrained hands immediately following reach training trials (white bars) and following the proprioceptive estimate trials (black bars) relative to baseline performance (i.e., errors achieved on the first day of testing after training with an aligned cursor were subtracted from errors achieved after reaching with a translated cursor). No-cursor reaches were significantly shifted in the direction of the distortion following translated-cursor training compared to aligned-cursor training (F (1, 33) = 45.60, $p < .001$). But as expected, the changes in open loop reaches varied depending on whether they were completed by the trained or untrained hand (F (1, 33) = 21.82, $p < .001$). However, given the low power of higher-order interactions, we were not able to find a significant 3-way interaction when including the factor of Group (F (1, 33) < 1, $p = .532$), nor a 4-way interaction when including Group and Time (F (1, 33) < 1, $p = .276$). Thus, we proceeded to our planned, pairwise comparisons for the trained hand and the untrained hand, in order to explore the difference in performance between aligned and translated training conditions, as a function of Group. In the next two paragraphs, we first report pairwise comparisons for the trained hand, and then untrained hand for each group.

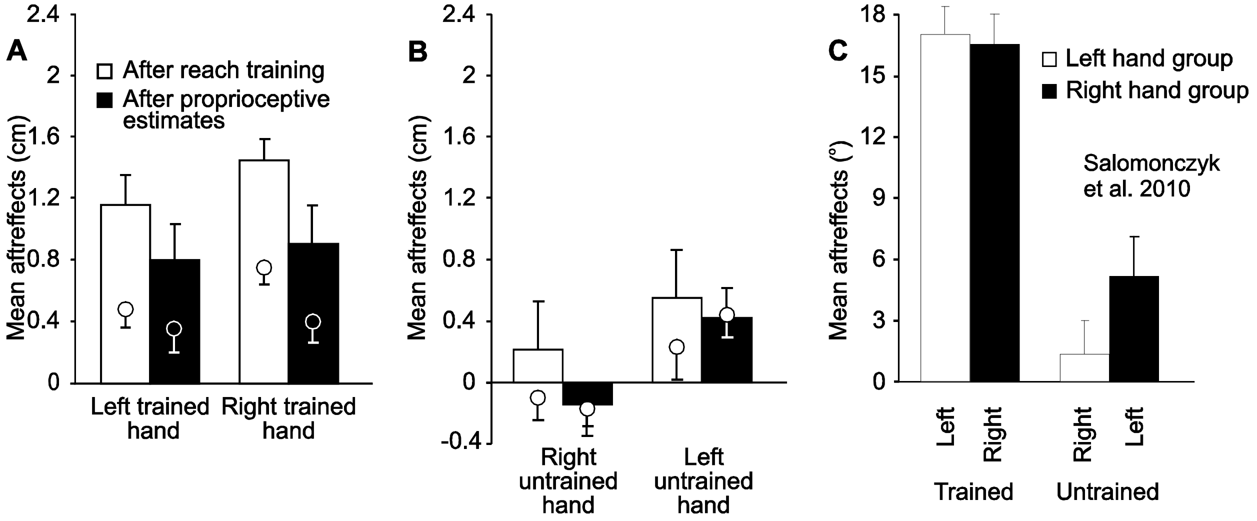

Figure 2.3 Mean endpoint aftereffects (*bars*) and errors at peak velocity (*circles*) following reach training with misaligned visual feedback of the hand. **a** Values reflect baseline-subtracted aftereffect errors in the trained left and right hands (*left* and *right bars,* respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **b** Values reflect baseline-subtracted aftereffect errors in the untrained right and left hands (*left* and *right bars,* respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **c** Mean endpoint aftereffects from (Salomonczyk et al. 2010) for (*left* and *right*) trained hands and (*right* and *left*) untrained hands (*left* and *right bars,* respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). *Error bars* reflect standard error of the mean

For the trained hands, the significant shift in no-cursor reaches for both the left and right hand was on average 1 cm (F (1,33) = 33.681, $p < .001$) and 1.2 cm (F (1.33) = 53.090, $p <$

.001), respectively . The fact that there was no further interaction across Groups (F (1, 33) < 1), suggest that this adaptation was achieved, and by a similar amount, for both the left and right trained hands. Analysis also revealed smaller reach aftereffects following the proprioceptive estimate trials compared to those immediately after the reach training trials (F (1, 33) = 4.512, *p* = .041). Specifically, reach aftereffects of 1.18 cm and 1.45 cm were observed in the first set of no-cursor reach trials (white bars in fig. 3A) for the left and right hands respectively, while the following set of no-cursor reaches (black bars in fig. 2.3A) revealed that reach aftereffects had diminished to 0.8 cm and 0.9 cm for the left and right hands, respectively. Despite the decay in reach aftereffects following the proprioceptive estimate trials compared to those immediately after reach training, the aftereffects for the trained hands were still significantly different from baseline conditions.

On the other hand, reaching errors in the untrained hand showed evidence of intermanual transfer only in the untrained left hand following opposite right hand adaptation (F (1, 33) = 5.412, *p* = .026), both when measured right before the proprioceptive estimate task and again right after, despite a small but non-significant decay in aftereffects over time (F (1,33) = 1.298, *p* = .263). Changes in reach endpoint for the untrained right hand did not differ following opposite left hand training (F (1, 33) < 1, *p* = .856). In other words, the untrained right hand (dominant hand) didn't benefit from the left hand (non-dominant) training, while, the left hand benefited from the dominant hand (opposite hand) training. Analysis of reach errors at peak velocity (as indicated by the circles in Fig 2.3A and 2.3B) revealed a similar pattern of results. Specifically, reach deviations at peak velocity in the untrained hand showed evidence of intermanual transfer only in the untrained left hand following opposite right hand adaptation (F (1, 33) = 4.896, *p* = .034), while reach errors at peak velocity for the untrained right hand did not differ following opposite left hand training (F (1, 33) < 1, *p* = .543). This suggests that endpoint accuracy and initial directional errors transferred between hands, but from right to left not from left to right.

In order to assess the extent of the intermanual transfer to the left untrained hand, we compared the aftereffects (for trials following both reach training and proprioceptive estimates) of this untrained hand with those of the trained left hand from the other group. We found endpoint reach errors in the untrained left hand were less than aftereffects of the trained left hand, but not significantly (t (33) =1.85, *p* = .073), while difference between the trained and untrained right hand were significant (t (33) = 4.38, *p* < .001). These findings confirm that the untrained left hand (non-dominant) benefited from previous training with the right hand (dominant) using a gradually-introduced translated cursor, however, the untrained right hand did not benefit from the prior training with the left hand.

Interestingly, Salomonczyk et al. (2010) found similar results in their study of intermanual motor transfer when they introduced a 30^{o} rotation to two subjects groups, one group which trained with the right hand and the other which trained with the left hand (Fig 2.3C). Specifically, after reaching with a rotated cursor subjects adapted their reaches in both the right and left trained hands (F (1,44) = 265.4, *p* < .001), however, only following right hand adaptation did the opposite untrained left hand show a significant difference in endpoint errors (5^{o}; F (1,44) = 7.646, *p* = .008). In other words, the right untrained hand did not differ following opposite left hand training (< 1^{o}; F (1, 44) < 1, *p* = .935). Also, analysis of reach errors at peak velocity revealed the same pattern of effects. These results suggest that prior training with the right hand led to a transfer of learning to the unexposed left hand.

2.4.2 Proprioceptive recalibration

2.4.2.1 Bias

Figure 2.4 depicts a 2 dimensional view of the positions at which subjects in the left (A) and right (B) hand training groups perceived their hands to be aligned with the reference markers after training with an aligned (empty symbols) and translated cursor (filled symbols) for the trained hand (squares) and untrained hand (triangles). While we found a significant change in proprioceptive biases after adapting to a translated cursor (F (1, 33) = 8.449, $p = .006$), we found no significant 3-way interaction including Hand used and Group (F (1, 33) < 1, $p = .529$) or 4-way interaction and including Hand used, Group and Reference marker (F (3, 99) = 1.062, $p > .05$). We then continued to our planned comparisons for the trained hand and the untrained hand in order to investigate the performance difference between aligned and translated training conditions, as a function of Group.

Following training with aligned cursor feedback, subjects estimated their trained hand was aligned with the reference marker when it was on average 1.17 cm to the right of it (left hand training group) or .46 cm to the left of it (right hand training group). After subjects trained with the translated cursor, the bias of their trained hand (squares) estimates of hand position shifted to the left, on average 0.65 cm, and thus in the direction of the visuomotor distortion (F(1,33) = 12.350, $p < .001$). The magnitude of this change is shown in the left bars in Fig 2.4C. This shift in proprioceptive estimates was comparable across the left and right hand training groups (F (1, 33) < 1, $p = .721$) and again comparable across the four reference markers (F (3, 99) = 2.019, $p = .150$), regardless of whether the center reference marker was proprioceptive or visual for the left ($p = 1$) and right hand ($p = .350$) training groups.

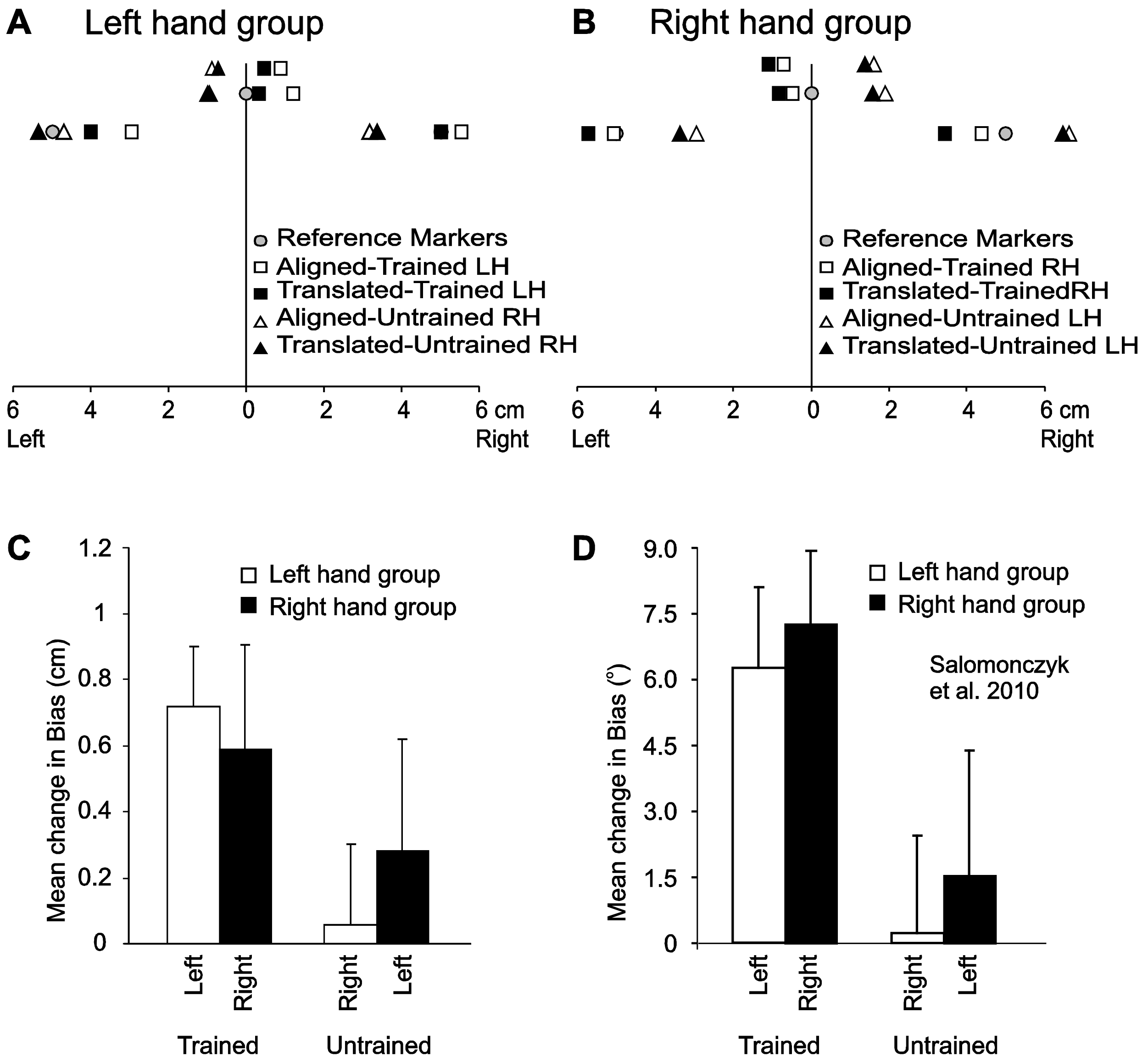

Figure 2.4 Proprioceptive estimates for the trained and untrained hands. **A** Left-hand training group mean 2D biases in the proprioceptive estimate tasks for the left trained (*squares*) and right untrained (*triangles*) hands following left-hand training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. The actual reference marker positions are represented as *filled gray circles*. **B** Right-hand training group mean 2D biases in the proprioceptive estimate tasks for the right trained (*squares*) and left untrained (*triangles*) hands following training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. Proprioceptive estimates relative to the body midline have been shifted above those made at visual markers for both **A** and **B** (*above*) to avoid overlap. **C** Mean change in bias for the (*left* and *right*) trained hands and (*right* and *left*) untrained hands (*left* and *right bars,* respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). **D** Mean change in bias from (Salomonczyk et al. 2010). *Error bars* reflect standard error of the mean

While the positions at which subjects felt their left and right trained hands (squares in Fig 2.4A and 2.4B) to be at a reference marker were significantly shifted following training with translated feedback, when we measured the untrained right and left hands, the mean biases were shifted only .05 cm and .27 cm leftwards (triangles in Fig 2.4A and 2.4B and bars on the right in Fig 2.4C), respectively. These shifts were not statistically significant from biases following training with the aligned cursor feedback (right hand: F (1, 33) < 1, p = .848; left hand: F (1, 33) < 1, p = .349).

Again, our findings are consistent with previous results observed by Salomonczyk et al.(2010) (Fig 2.4D). Specifically, they found that the position at which subjects' felt their trained hand coincided with the reference marker was shifted leftwards by 6.6^{o} (approximately 20% of the distortion introduced) after training with a 30^{o} rotated cursor compared to after reaching with an aligned cursor (F (1, 44) = 28.8, p < .001). While, the mean biases in the untrained left and right hands were shifted by 1.50^{o} and $.14^{o}$ leftwards, respectively, however, these shifts were not statistically significant (F(1,44) <1, p = .953; F(1,44) < 1, p = .564, respectively).

2.4.2.2 Uncertainty

Figure 2.5 depicts the magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (white bars) and translated (white dashed bars) cursor feedback, and the right and left untrained hands following reach training with aligned (black bars) and translated (black dashed bars) cursor feedback. The uncertainty ranges did not differ across any of the factors; nor were there any interactions (p > 0.05).

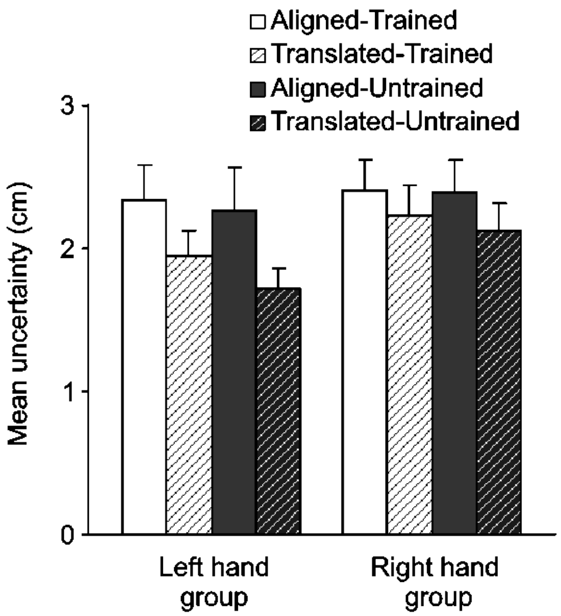

Figure 2.5 Magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (*white bars*) and translated (*white dashed bars*) hand-cursor feedback. Magnitude of uncertainty ranges for the right and left untrained hands is also displayed following reach training with aligned (*black bars*) and translated (*black dashed bars*) cursor feedback. *Error bars* reflect standard error of the mean

2.5 Discussion

We sought to assess the extent that adapting to a translated cursor leads to transfer of motor adaptation to the opposite hand, and whether this transfer differs between the dominant and non-dominant hands. Additionally, we wanted to determine whether changes in hand proprioception that occur with the trained hand following motor adaptation transfer to the untrained hand. We found intermanual motor transfer to the left untrained hand after subjects trained their right hand to reach with translated visual feedback of their hand, while transfer from the left trained hand to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike motor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

2.5.1 Motor transfer and arm asymmetry

While visuomotor adaptation was observed to the same extent in both the left and right trained hands of right-handed individuals following adaptation to a visuomotor distortion, these findings were not symmetrically transferred to the untrained hands. Small but significant reach aftereffects were observed in the untrained left hand following training with the right hand, suggesting some of the motor adaptation of the right hand had been transferred to the untrained left hand. Unsurprisingly, these transferred aftereffects were smaller than those observed in the trained left hand, suggesting that transfer between the two hands is incomplete. No transfer of reach aftereffects were observed in the untrained right hand following training with the left hand. Our results are consistent with previous findings from our lab (Salomonczyk et al. 2010), in which a different distortion was employed. Salomonczyk et al. found that subjects adapted their reaches in both the right and left trained hands (and with comparable magnitude) after training with a 30 ^{o} CW rotated cursor; however, intermanual transfer only occurred after right hand adaptation and only the untrained left hand produced significant aftereffects. Together these results suggest the asymmetry in transfer is not due to the type of distortion (i.e., translated or rotated cursor), as it occurred in both cases. While adaptation to a translated cursor may result in greater generalization overall (Ghahramani et al. 1996; Vetter et al. 1999; Cressman and Henriques 2009), it did not result in greater or different patterns of intermanual transfer compared to that produced following adaptation to a comparably sized visuomotor rotation (Salomonczyk et al. 2010). Specifically, from the aftereffects observed in the present study and those by Salomonczyk et al.'s (2010) (Fig 2.3C), it appears that there were no real differences in the size and pattern of the intermanual motor regardless of the extent of motor adaptation achieved.

Our pattern of intermanual motor transfer, based on measuring changes in endpoint errors in the open-loop reaches (i.e., aftereffects) is different from that found by Sainburg and Wang (2002; 2003; 2011) when assessing how well the untrained hand could adapt to the same perturbation experience by the trained hand. The authors found that adaptation of both the untrained left and untrained right hand were facilitated with prior training with the opposite hand to the same visuomotor rotation. However, the measures by which these two untrained arms showed this advantage, or transfer, differed depending on the arm. Specifically, final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. The asymmetries in their studies differ from our own in that we found evidence of transfer of initial directional accuracy and final position accuracy to the non-dominant hand while we also failed to observe either effect from the non-dominant to the dominant hand. The difference between our studies (including that by Salomonczyk et al.(2010)) and theirs may have to do with how we assessed adaptation and transfer. In Sainburg and Wang's (2002) paradigm, as well as other studies on intermanual transfer, the untrained hand was exposed to the distortion and the learning rate (across trials) was assessed. Intermanual transfer is indicated by a steeper learning rate (also known as savings) as well as a smaller deviation in the first trials with the untrained hand following opposite-hand training. However, we assessed intermanual transfer by examining directional errors at peak velocity and endpoint errors during open-loop reaches to determine the magnitude of transfer. One explanation for this inconsistency , as outlined above, could be that direction and pattern of asymmetry of intermanual transfer differs depending on the measures of assessment. However, research from our lab using a different paradigm (Balitsky Thompson and Henriques 2010) where intermanual transfer was assessed by measuring facilitation following opposite hand training, revealed facilitation only from the right (dominant) arm to the left (non-dominant) arm. This pattern of transfer occurred across different magnitudes of distortion (45°, 60°, 75°) and different feedback representations (cursor vs. video image of the hand). Thus, this motor transfer to only the non-dominant arm found in three of ours studies (separate subjects and even different equipment for the Balitsky Thompson and Henriques study) may be beyond merely how transfer was measured, or the extent of motor adaptation. Another possible explanation of these different results in our study and studies of Sainburg and Wang is that the magnitude of aftereffects in our study was around 30 % of the visuomotor distortion, so that learning may not have been complete, and thus may have influenced the direction and the extent of the intermanual transfer.

Our observed asymmetric transfer is similar to transfer found by Redding and Wallace (2008) following adaptation to displacing prisms. The authors found that aftereffects (as assessed by reaches made following removal of the prisms) transferred from the right trained hand to the left untrained hand but not vice versa. The magnitude of transfer, as in our study, was approximately one-third of the aftereffects observed in the trained hand. These authors suggest that this asymmetric transfer between the right and left trained hands is due to symmetrically lateralized limb control but asymmetrical spatial mapping, where the right limb is represented in both hemispheres while the left limb is represented only in the right hemisphere (Corbetta et al. 1993; Farne et al. 2003; Butler et al. 2004). The asymmetrical motor transfer of reach aftereffects we observe in the current study is consistent with this proposal.

2.5.2 Proprioceptive transfer and arm symmetry

We used a sensory estimation task that did not require any goal-directed movements, to assess proprioceptive recalibration independent of motor changes. Our findings replicate those from previous studies (Cressman and Henriques 2009; 2010; Cressman et al. 2010; Salomonczyk et al. 2011) in that subjects experienced a shift in the position at which they felt their hand was aligned with a reference marker by roughly 20% of the visuomotor distortion. However, proprioceptive recalibration did not transfer from the dominant or non-dominant trained to the opposite untrained hand. In particular, the mean biases of the untrained right and left hands were shifted only .05 cm and .27 cm leftwards, respectively, following reach training with a translated cursor compared to reach training with an aligned cursor, and these shifts were not statistically significant. Training with rotated visual hand feedback revealed a similar lack of transfer between the hands. Specifically, when Salomonczyk et al. (2010) introduced a 30° rotation to left and right-hand trained groups, the authors found that subjects recalibrated proprioception equivalently in both groups, while the mean biases remained unchanged following opposite hand training. Of course, given that proprioceptive change is much smaller than the change in reach movements (aftereffects) following visuomotor adaptation, it is possible that the felt position of untrained hand is shifted but by an amount that it is too small to detect. The magnitude of proprioceptive recalibration is typically a third of the aftereffects (Cressman and Henriques 2009; 2010), and in this study, the relative change in felt position for the trained hand (compared to the aftereffects) was closer to 70%. Thus, given that aftereffects produced with the untrained left hand were about 0.6 cm in size, then the 33% change in the proprioceptive perception of this hand would be about 0.2 cm, while a 70% change would be closer to 0.4 cm. Indeed, we do find that the change in bias of the left hand was closer to 0.4 cm, (see right black bar in Fig 2.4C). However, given that this shift was not large enough to be detected statistically, we must conclude that hand proprioception was not changed for the untrained hands.

We assume that changes in biases of the trained hand following reach training are due to changes in proprioceptive estimates of the trained hand and not to some changes in the representation of visual space. This is based on the fact that in the current study, as well as in previous results, we have shown change in perceived hand position is equivalent between visual or proprioceptive (the body midline) markers (Cressman and Henriques 2009; Salomonczyk et al. 2011). The present results further argue against a possible shift in the visual representation of space following adaptation, as changes in bias for the trained and untrained hands would be similar if the visual representation of the marker was shifted. Indeed, this was not observed.

Several studies have suggested that the two arms may be specialized at using different types of sensory information for localizing a target. For instance, Goble and Brown (2008) have suggested that the left limb is better at matching proprioceptive targets and the right limb for matching visual targets. However, we did not find similar asymmetries between the two hands in our sensory task. Moreover, Carson et al. (1990) and Jones et al. (2010; 2012) found that right handed participants estimated their hand location with error magnitudes between the two hands, although errors were opposite in direction. Additionally, Jones et al. (2010; 2012) reported that the magnitude of proprioceptive biases and uncertainty ranges across the two hands, measured without a preceding reach-training task, did not differ at all. In the present study, we found the same magnitude of proprioceptive biases when subjects judged the right hand with respect to a body midline (i.e., proprioceptive) and visual reference markers.

In summary, we found no arm-dependent differences in either proprioceptive estimates or unseen hand movements made to visual targets. Moreover, given that we did not find evidence of proprioceptive recalibration transferring between hands, it appears that unlike visuomotor adaptation, proprioceptive recalibration is specific to the hand exposed to the distortion. Further studies are required to characterize motor adaptation and sensory recalibration and determine the extent that these two processes are responsible for intermanual transfer of motor adaptation.

CHAPTER THREE

GENERALIZATION OF REACH ADAPTATION AND PROPRIOCEPTIVE RECALIBRATION AT DIFFERENT DISTANCES IN THE WORKSPACE

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Denise Y. P. Henriques

Experimental Brain Research

3.1 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., ~22.5°; Krakauer et al.(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 work space. 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 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.

3.2 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 have 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 uniformed 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 on the hand. 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 (Abeele & Bock, 2001; Cressman & Henriques, 2009; Ghahramani et al., 1996; Ghilardi, Gordon, & Ghez, 1995; Krakauer et al., 1999; Wolpert, Ghahramani, & Jordan, 1995). 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) (Baraduc & Wolpert, 2002; Ghahramani et al., 1996; Krakauer et al., 1999; Vetter, Goodbody, & Wolpert, 1999; Wang & 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 (Ghahramani et al., 1996; Ghilardi et al., 1995; Imamizu et al., 1995; Krakauer et al., 2000; Pearson et al., 2010; Poggio & Bizzi, 2004). 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; Neva & Henriques, 2013; Pearson et al., 2010; Wang & Sainburg, 2005). 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 8 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 & Cressman, 2012). Changes in felt hand position (or proprioceptive recalibration) have been studied in our lab 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 (Mattar, Darainy, & Ostry, 2013; Ostry, Darainy, Mattar, Wong, & Gribble, 2010).

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 existence in the case of deafferented patients (Bernier, Chua, Bard, & Franks, 2006; Ingram et al., 2000), subjects still adapt their movements in response to a visual distortion (Bock & Thomas, 2011; Pipereit, Bock, & Vercher, 2006).

In accordance with these findings, Cressman and Henriques (2015) have shown that the generalization patterns of proprioceptive recalibration and reach adaptation are different. Specifically, Cressman and Henriques (2015) 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 and colleagues (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.

3.3 Methods

3.3.1 Subjects

In total, 13 right-handed subjects (mean age = 22, SD = 2.34, 7 males and 6 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 towards an undergraduate psychology course.

3.3.2 General experimental setup

The experimental setup is illustrated in Fig. 3.1A. 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 72Hz) 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 set-up and subjects' shoulders.

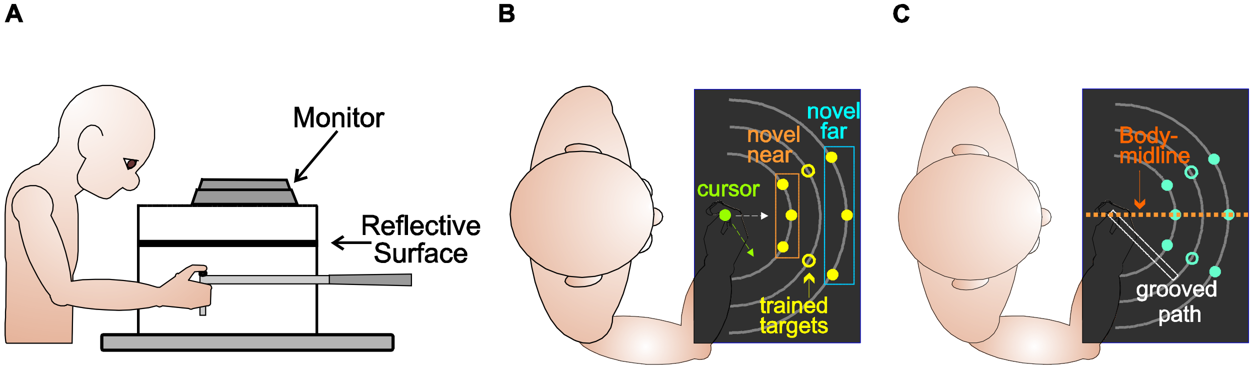

Figure 3.1 Experimental setup and design. **A** Side view of the experimental setup. **B, C** Top view of experimental surface visible to subjects. The home position was located approximately 20 cm directly in front of subjects' midline and is represented by a hand cursor (1-cm-diameter *green disk*) 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)

3.3.3 Procedure

Similar to our previous studies (Mostafa, Salomonczyk, Cressman, & Henriques, 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 were aligned with the hand (for baseline measures) while on the second testing day, the cursor was rotated 45° clockwise (CW) relative to their 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. 3.2.

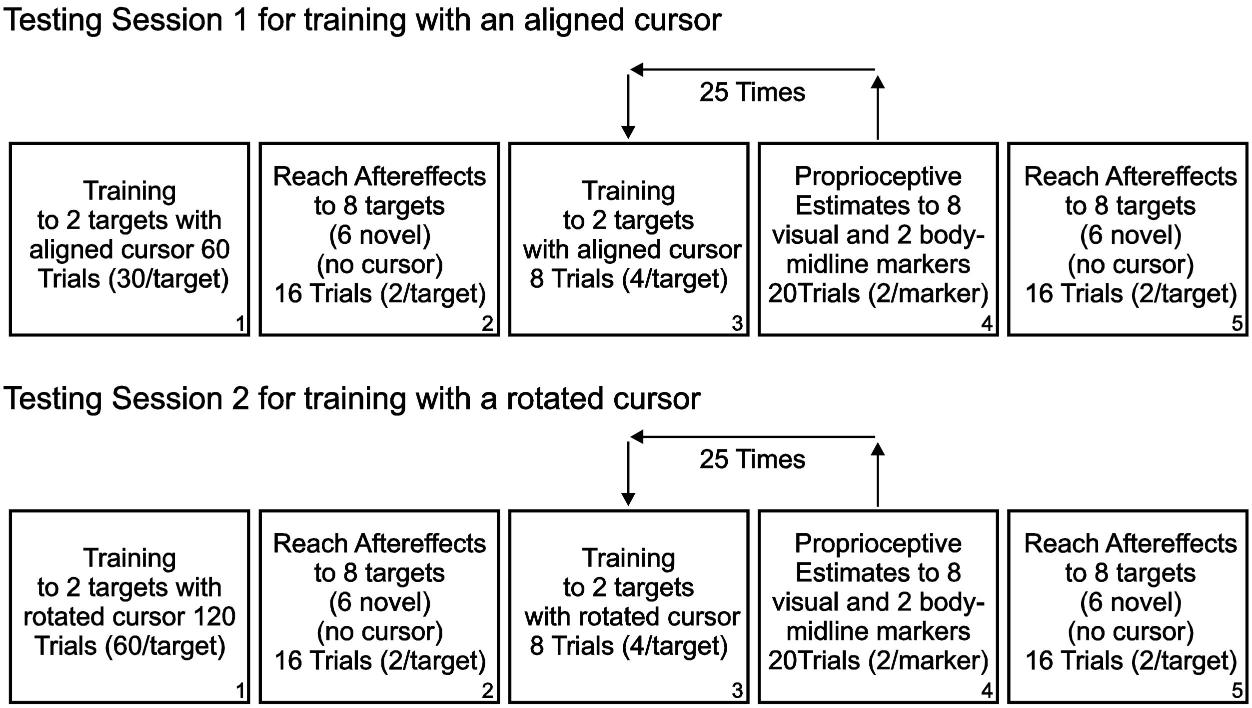

Figure 3.2 Schematic showing the order in which the tasks were completed within a testing session. Both testing sessions followed the same order of tasks. The difference between the sessions was the visual feedback provided in the reach training tasks. The cursor was either aligned with the hand (*session 1*) or rotated 45° clockwise (CW) relative to the hand (*session 2*)

3.3.3.1 First testing session tasks

Aligned reach training task:

The first testing session included aligned reach training trials (boxes 1 and 3 in Fig. 3.2), where subjects were asked to reach (as quickly and accurately as possible) to a visual yellow target disc (1 cm in diameter, Fig. 3.1B) with their right hand hidden from view, but represented by a cursor (green disc, 1 cm in diameter, Fig. 3.1B) located directly above their thumb. In front of the home position, which was located approximately 20 cm in front of subjects, there were 2 reach targets located radially 13 cm from the home position at 30° left (CCW) and 30° right (CW) of centre (Fig. 3.1B). The reach trial was considered complete when the center of the cursor had moved to within 0.5 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 6 novel targets 2 times each without a cursor (no-cursor reach trials, Boxes 2 and 5 in Fig. 3.2). 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 discs, Fig. 3.1B). 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. 3.2) 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. 3.1C (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 (2 are the trained locations and 6 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 if their hand was to the right or left of the reference marker (using the right or left arrow keys on a keyboard). The ten 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 discs, Fig. 3.1C). Two of the ten 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. 3.2). Subjects began by completing an additional 8 reach training trials with a cursor to the reach training targets located 13 cm at 30º 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 8 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.

3.3.3.2 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 3.2). In this misaligned reach training task, the cursor was gradually rotated 45° rightwards (CW, 0.75° 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.

3.3.4 Data analysis

3.3.4.1 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), were analyzed to determine if 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 if 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 2 Visual Feedback condition during the reach training task (i.e., aligned vs. rotated cursor) x 2 Epoch (trials completed before vs. after the proprioceptive estimate task) x 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 (2 trained sites vs 6 or 8 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).

3.3.4.2 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 ($\alpha = 0.05$).

3.4 Results

3.4.1 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 figure 3.3 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.

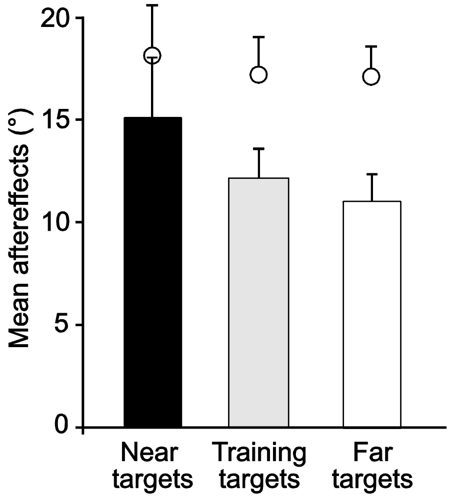

Figure 3.3 Reach aftereffects: difference in mean angular reach endpoint error for the no-cursor reaches after training with misaligned visual feedback for training targets, novel-near targets, and novel-far targets relative to baseline performance. *Circles* represent mean changes in reaching errors at peak velocity. *Error bars* reflect the standard error of the mean (SEM)

More interestingly, we found that the extent of reach adaptation for the trained targets [(12.2°), Fig. 3.3, left gray bar] and for the novel targets [(15.1° and 11° 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 generalization across novel targets locations, in that change in angle at peak velocity did not differ between trained and novel targets (F (2, 24) = .325; *p* = .622).

3.4.2 Proprioceptive recalibration generalizes to a lesser extent at far distances

Figure 3.4A depicts a 2 dimensional view of the positions at which subjects perceived their hands to be aligned with the reference markers (grey 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 significant shifted by 8.5° 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°, while the change was 9.4° and 6.3° at the novel-near and novel-far reference markers locations, respectively (Fig. 3.4B). 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 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. 3.4C), 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). 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.

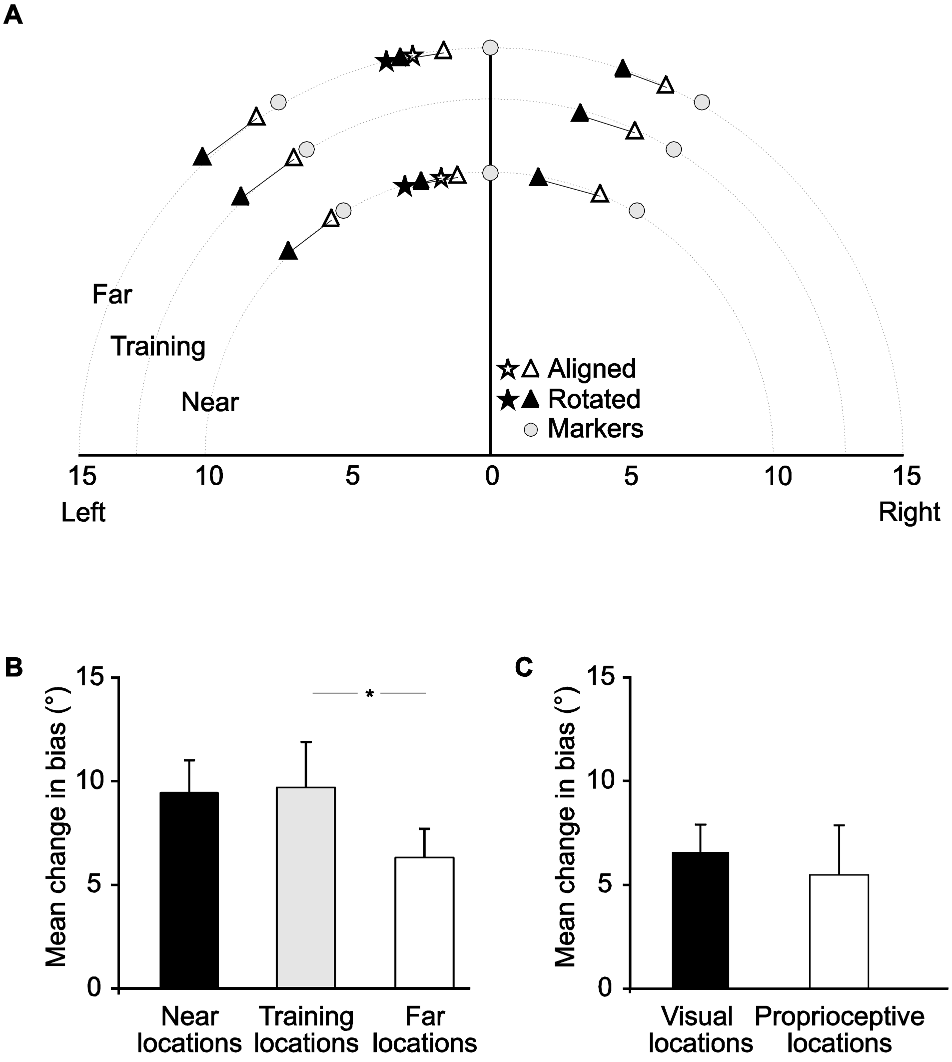

Figure 3.4 Proprioceptive biases following training with aligned and rotated visual feedback of the hand. **A** Mean 2D biases in the proprioceptive estimate tasks relative to the reference marker locations (*gray disks*) after training with aligned visual feedback (*unfilled symbols*) and after training 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 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

3.5 Discussion

Our goal was to determine whether proprioceptive recalibration, like reach adaptation, generalizes to locations at different distances across the work space. 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.

3.5.1 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 lab (Clayton, Cressman, & Henriques, 2014; Salomonczyk et al., 2011). 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 & 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 8 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, Matter 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, Matter 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. Matter and Ostry(2010) proposed that the inconsistency between their results and the results of Krakauer et al's (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 (1998b) 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, 2015).

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 (Krakauer et al., 2000; Pine et al., 1996). 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 Rugy, 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.

3.5.2 Proprioceptive acuity across the workspace

Following training with an aligned cursor, our subjects perceived their unseen hand position to be slightly rightwards of its actual position. Indeed, with no reach training, the same pattern has been observed previously in our lab (Jones et al., 2010; Jones et al., 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 centimeter 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).

3.5.3 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 lab (Cressman & 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 (Izawa et al., 2012; Synofzik et al., 2008). In addition, other studies have observed changes to subjects' sense of hand motion after reach adaptation to a velocity-dependent force field (Mattar et al., 2013; Ostry et al., 2010; Vahdat, Darainy, Milner, & Ostry, 2011).

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 & Cressman, 2012).

Cressman and Henriques (2015) 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 degrees) 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 are processed differently in the brain.

3.5.4 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 (2015) 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.

CHAPTER FOUR

MOTOR LEARNING WITHOUT MOVING: PROPRIOCEPTIVE AND PREDICTIVE HAND LOCALIZATION AFTER PASSIVE VISUOPROPRIOCEPTIVE DISCREPANCY TRAINING

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PLoS One (in revision)

4.1 Abstract

An accurate estimate of limb position is necessary for movement planning. Where we localize our unseen hand after a reach depends on felt hand position, or proprioception, but this is usually neglected in favour of predicted sensory consequences based on efference copies of motor commands. Both sources of information should contribute, so here we set out to further investigate how much of hand localization depends on proprioception and how much on predicted sensory consequences. We use a passive training paradigm with rotated visual feedback that eliminates the possibility to update predicted sensory consequences, but still recalibrates proprioception. Localizing an unseen hand after self-generated movements uses both efference-based predictions as well as afferent proprioceptive signals, but after robot-generated movements only proprioception is available. We find direction changes in open-loop reaches as well as shifts in hand localization, both after robot- and self-generated hand movements. Both motor and proprioceptive changes are only slightly smaller as those after training with self-generated movements, confirming that proprioception plays a large role in estimating limb position and in planning movements.

4.2 Introduction

Sensory information is central to how we control all our movements. Our brain is even thought to use *predicted* sensory consequences derived from efferent copies of motor commands for motor control (Duhamel, Colby, & Goldb, 1992). When training with rotated visual feedback of the hand, we update these predictions (Wolpert, Ghahramani, & Jordan, 1995). Additionally, such training leads to a recalibration of our sense of felt hand position - "proprioception" - to be more aligned with the distorted visual feedback (Cressman & Henriques, 2009). Both of these changes have been measured by asking people to localize where their unseen hand is – before and after training (Clayton, Cressman, & Henriques, 2013; Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Jones, Fiehler, & Henriques, 2012; Synofzik, Lindner, & Thier, 2008; Yavari et al., 2016). While our lab has previously found that proprioception accounts for a large portion of the change in hand localization ('t Hart & Henriques, 2016), it is far from clear how much each process contributes or how to tease them apart. Here we use passive training, that removes the need to update predicted sensory consequences, in an attempt to isolate the contribution of proprioception to hand localization.

The predicted sensory consequences of movements may play several important roles in motor control. Predicted sensory consequences allow us to correct our movements before sensory error signals are available, they can be used to select movements that best achieve our goals and they may inform us on the location of our limbs. Hence measuring predicted sensory consequences is valuable in movement research. In visuomotor rotation adaptation tasks, the actual sensory outcome is systematically different from the expected outcome, so that participants update the predictions on the outcome of the trained movements. In previous experiments, people were asked to make a movement and then indicate the location of, or "localize," their unseen, right hand, before and after training with rotated visual feedback (Izawa et al., 2012; Synofzik et al., 2008). Since there was no visual information available to the participants, the predicted sensory consequences of the movement should be used in localizing the unseen hand. Both studies found a significant shift in hand localization, providing evidence that predicted sensory consequences are indeed updated as a result of visuomotor rotation adaptation.

However, our lab has shown that our sense of where we feel our hand to be, proprioception, is also reliably recalibrated after visuomotor rotation adaptation (Barkley, Salomonczyk, Cressman, & Henriques, 2014; Cressman & Henriques, 2009; Cressman, Salomonczyk, & Henriques, 2010; Henriques & Cressman, 2012; Henriques, Filippopulos, Straube, & Eggert, 2014; Maksimovic & Cressman, 2018; Mostafa, Kamran-Disfani, Bahari-Kashani, Cressman, & Henriques, 2015; Mostafa, Salomonczyk, Cressman, & Henriques, 2014; Nourouzpour, Salomonczyk, Cressman, & Henriques, 2014; Salomonczyk, Cressman, & Henriques, 2011). This has also been shown by other labs (Cameron, Franks, Inglis, & Chua, 2012) and a comparable proprioceptive change is induced with force-field adaptation (Ostry & Gribble, 2016). As proprioception also informs us on the location of our limbs, we have on occasion used a task that is very similar to hand localization to investigate this (Clayton, Cressman, & Henriques, 2014; Cressman & Henriques, 2009; Jones et al., 2012; Ruttle, ’t Hart, & Henriques, 2018). Although proprioceptive recalibration has been largely ignored as an explanation for changes in hand localization, we and others have shown that it accounts for a substantial part of the changes in localization, along with updates in predicted sensory consequences (’t Hart & Henriques, 2016; Cameron et al., 2012). Nevertheless, it is far from clear how much proprioception and prediction each contribute to hand localization.

Here we intend to further examine the contribution of proprioception to hand localization. To do this, we use passive training where a robot arm moves the participants' arm out so that the cursor always directly goes to the target (Cameron et al., 2012; Cressman & Henriques, 2010; Salomonczyk, Cressman, & Henriques, 2013). This means there is no efference copy available and no visuomotor error-signal, both of which are required to update predicted sensory consequences. However, there is a discrepancy between vision and proprioception that drives proprioceptive recalibration. Thus, changes in hand localization after this type of training should be due to proprioceptive recalibration only. We use the same experimental protocal as before ('t Hart & Henriques, 2016), so that we can compare localization shifts between the two different types of training, and can better assess the contributions of predicted sensory consequences and proprioception to hand localization.

4.3 Methods

We set out to test the relative contributions of proprioception and efference-based prediction to hand localization. We use visual training with robot-generated hand movements to prevent updates of predicted sensory consequences, but still elicit proprioceptive recalibration.

4.3.1 Participants

Twenty-five right-handed participants were recruited for this study. One participant was excluded for not following task instructions, and three were excluded for low performance on a task that ensures attention during the passive training. All analyses presented here pertain to the remaining twenty-one participants (mean age: 20.1±2.3, 13 females and 8 males), but the data of the three low-performing participants is included in the online dataset (https://osf.io/zfdth/). All had normal or corrected-to-normal vision, and provided prior, written informed consent in accordance with the ethical guidelines set by the York Human subjects Review Subcommittee and received credit toward an undergraduate psychology course. Participants were screened verbally, and all reported being right handed and not having any history of visual, neurological, and/or motor dysfunction.

4.3.2 Setup

Participants sat in a height-adjustable chair to ensure that they could easily see and reach all targets presented on a reflective screen (see Fig 4.1). During all tasks, they held 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. A monitor (Samsung 510 N, refresh rate 60 Hz) was mounted 11 cm above the reflective screen, such that images displayed on the monitor appeared to lie in the horizontal plane where the right hand was moving. The reflective screen was mounted horizontally 18 cm above the robot manipulandum. A touch screen was mounted 13 cm underneath the reflective surface, so that subjects could indicate the location of the unseen right-hand locations (specifically the unseen thumb) with their visible left hand, which was lit up with a small spot light (only in localization tasks). The room lights were dimmed and the participants' view of their right hand was blocked by the reflective screen, as well as a dark cloth draped between the touch screen and participants' right shoulder.

4.3.3 Procedure

The first part of the experiment used training with a cursor aligned with the hand and the second part had training with a cursor rotated around the start position (Table 1). During the training with rotated feedback, the cursor was gradually rotated 30° clockwise. This introduces a discrepancy between the actual, or felt, hand position and the visual feedback, that should evoke proprioceptive recalibration. However, the movements are robot generated, so that there are no predicted sensory consequences based on the outgoing motor command. Hence the prediction errors that are thought to lead to motor learning are absent as well. After both types of training, open-loop reaches as well as two kinds of hand localization tasks were done to test the effect of training on proprioceptive and predictive hand estimates.

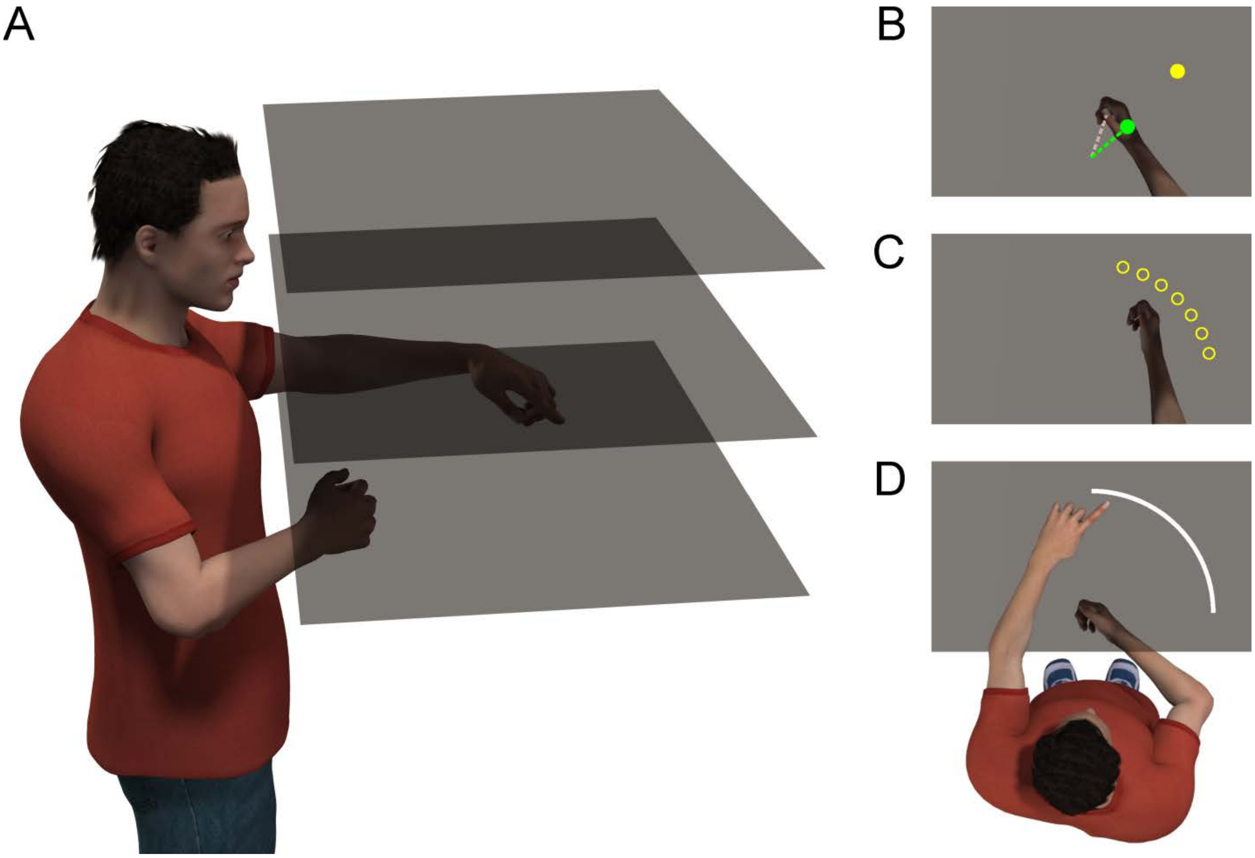

Figure 4.1 **a)** Participants moved their unseen right hand with visual feedback on hand position provided through a mirror (*middle surface*) half-way between their hand and the monitor (*top surface*). A touchscreen located just above the hand was used to collect responses for the localization tasks (*bottom surface*). **b)** Training task. The target, shown as a yellow disc, is located 10 cm away from the home position at 45°. In the rotated training tasks, the cursor (shown here as a green circle) represents the hand position rotated 30° relative to the home position. **c)** No-cursor reach task. Targets are located 10 cm away from the home position at 15°, 25°, 35°, 45°, 55°, 65°, and 75°, shown by the yellow circles here (only one was shown on each trial). While reaching to one of these targets, no visual feedback on hand position is provided. **d)** Localization task. The participants' unseen, right hands moved out, and subsequently participants indicated the direction of the hand movement by indicating a location on an arc using a touch screen with their visible left index finger.

4.3.3.1 Exposure training

In what we call 'exposure training' the participants did not move their hand toward the target, but the robot did. In this task (Table 1, white rows), the right hand was represented by a cursor (green disk, 1 cm in diameter, Fig 4.1b) located directly above participant's thumb. The robot moved the participant's unseen right hand (and the cursor) along a direct path toward a visual yellow target disk and back to the starting position (1 cm in diameter, Fig 4.1b). The home position was located approximately 20 cm in front of subjects and the visual target located 10 cm from the home position at 45° (Fig 4.1b). In order to make sure participants were paying attention to the cursor, the cursor was switched of for 2 screen refreshes (~33.3ms) on 50% of the trials at a random distance between 4 and 9 cm from the home position and participants were asked to report this using a button press with the left hand. Performance on this task was used to screen participants.

During the first half of the experiment, the cursor and hand path were aligned during exposure training. In the second part of the experiment, the "rotated" session, the same training target at 45° was used, and the cursor kept moving straight to this target. However, the robot-generated hand path gradually rotated 30° CCW (Fig 4.1b) with respect to the visible target and the cursor in increments of 0.75°/trial, so that the full rotation was reached after 45 trials. This mimics error-free responses to a gradual visuomotor rotation of 30° CW. The initial training consisted of 50 trials in the aligned part and 90 in the rotated part. In between open-loop reach tasks and localization tasks (Table 1, all gray rows) extra training tasks were done, each of which consisted of 10 trials in the aligned part of the experiment and 60 trials in the rotated part.

4.3.3.2 No-cursor reaching

The trials in no-cursor reaching (Table 1, light gray rows) serve as a classical measure of motor adaptation. On each of these trials participants were asked to reach with their unseen right hand to one of 7 visual targets, without any visual feedback on hand position. The targets were 10 cm from the home position, located radially at: 15°, 25°, 35°, 45°, 55°, 65°, and 75° (Fig

4.1c). A trial started with the robot handle at the home position and, after 500 ms, the home position disappeared and the target appeared, cuing the participants to reach for the target. Once the participants thought they had reached the target they held their position for 250 ms, and the target and the home position disappeared, cuing participants to move back to the home position along a straight, constrained path to begin the next trial. If participants tried to move outside of the path, a resistance force, a stiffness of 2 N/(mm/s) and a viscous damping of 5 N/(mm/s), was generated perpendicular to the path. In every iteration of the no-cursor reach task, each target was reached three times, for a total of 21 reaches in pseudo-random order. The no-cursor reaching task was performed four times in the aligned part of the experiment and five times in the rotated part of the experiment.

4.3.3.3 Localization

In this task (Fig 4.1d; Table 1, dark gray rows) participants indicated where they thought their unseen right hand was after a movement. First, an arc appeared, spanning from 0° to 90° and located 10 cm away from the home position and the participants' unseen, right hand moved out from the home position in a direction somewhere within the arc. The hand was stopped by the robot at 10 cm from the home position and then, to prevent the online proprioceptive signals from overriding the predictive signals ('t Hart & Henriques, 2016; Izawa et al., 2012), the hand was moved back to the home position using the same kind of constrained path as used for the return movements in the no-cursor task. Participants indicated with the index finger of their visible, left hand on the touch screen mounted directly above the robot handle where they thought their trained hand had crossed the arc.

Crucially, there were two variations of this task. First, in the 'active' localization task participants generated the movement themselves, as they could freely move their unseen right hand from the home position to any point on the arc. Second, there was a 'passive' localization task where the robot moved the participants' hand out and back, to the same locations the participants moved to in the preceding 'active' localization task in a shuffled order (hence, active localization is done first). In active localization, participants have access to both proprioceptive information as well as an efference-based prediction of sensory consequences, but in passive localization, only proprioception should be available. The active and passive localization task each consisted of 25 trials, and each of the tasks was done a total of four times; twice after aligned and twice after rotated training.

4.3.3.4 Classic training

The paradigm described above is an exact replica of a paradigm we used earlier ('t Hart & Henriques, 2016) with two exceptions. First, we used exposure training here, instead of the standard reach training with volitional movements, which we will call 'classic' training. Second, all localization is delayed until the right hand has returned to the home position in this study (see Table 1), so that instead of both delayed and online localization we have two repetitions of each delayed localization task. With this paradigm we can compare changes in localization and no-cursor reaches change after exposure training with changes in the same measures after classic visuomotor adaptation training.

4.4 Analyses

Prior to any analyses, both the localization responses and the no-cursor reach data were visually inspected and trials where the participants did not follow task instruction were removed (e.g., several movements back and forth, or a touch-screen response on the home position, instead of on the white arc).

4.4.1 Localization

Localization responses were taken as the (signed) angular difference between vectors through the home position and the actual hand position as well as the location indicated on the touch screen. Prior to analyses, idiosyncratic differences in performing this task were countered. Before conversion to degrees angle, a circle with a 10 cm radius was fit to the touch screen responses of each participant and the offset of this circle's centre was subtracted from all response coordinates, so that all responses fell close to the arc. Then, a smoothed spline was fit to every participant's response errors in each of the four localization tasks (aligned vs. rotated and active vs. passive) and these were used to obtain localization errors at the same locations used for the no-cursor reaches (15°, 25°, 35°, 45°, 55°, 65° and 75°), but only if that location fell within the range of the data (i.e., we only interpolate). This way localization responses could be compared across participants despite the freely chosen reach directions. At the 15° degree location 7/21 participants didn't have an estimate in one or more of the four localization tasks (in the "classic" data it was also 7/21). While that data is shown in the figures, we did not use it for analysis.

First we test if localization responses shifted following rotated exposure training compared to aligned. We then test if the shift in localization responses is different for active and passive localization, and we run analyses comparing localization after exposure training with localization after "classic" training. Finally, we explore the generalization of localization responses and if they are different between the groups doing classic and exposure training.

4.4.2 Reach aftereffects

To assess any reach adaptation that may have occurred after exposure training we analyzed reach endpoints errors in no-cursor trials. Reach endpoint errors were the (signed) angular difference between a vector from the home position to reach endpoint and a vector from the home position to the target. We obtained reach aftereffects by subtracting reach endpoint errors after aligned training from those after rotated training. No-cursor endpoint errors were analyzed to see if participants adapted the direction of their reaching movements after rotated exposure training. We also tested if any such change decayed, i.e., if it was the same immediately after exposure training, or when a localization task was done in between exposure training and no-cursor reaches. Furthermore, we test if the generalization of reach aftereffects is different between exposure and classic training and if there is any generalization of reach aftereffects.

Pre-processing and analyses were done in R 3.4.3 (Team, 2017) using lme4, lmerTest and various other packages. Most analyses used linear mixed effects models, since there is some missing localization data. These are “converted” to more readable ANOVA-like output, using a Satterthwaite approximation (Luke, 2017). Highly similar results are obtained with a Chi-square approximation. Data, scripts and a notebook with analyses (Mostafa, ’t Hart, & Henriques, 2017) are available on the Open Science Framework (https://osf.io/zfdth/) and GitHub (https://github.com/thartbm/exposureconsequences).

In short, this experiment allowed us to test how mere exposure to a visual-proprioceptive discrepancy changes both reach aftereffects and hand localization responses, and compare them with those obtained after more regular, “classic” training.

4.5 Results

In this study we intend to further elucidate the relative contributions of (updated) predicted sensory consequences and (recalibrated) proprioception to hand localization. We can parcel out these contributions by measuring hand localization after both robot-generated and self-generated movements. Finally we compare the data from the current experiment with those obtained in an earlier study that used an identical paradigm, but trained with self-generated movements, or “classic” training.

4.5.1 Localization

First we test our hypothesis that exposure training does not lead to changes in predicted sensory consequences. Since the difference between active and passive localization stems only from the presence or absence of predicted sensory consequences, there should be no difference between the two if predicted sensory consequences are not changed by exposure training. At first glance, it seems there might be a difference between active and passive localization shifts in exposure training (see Fig 4.2a), although it is smaller than in classic training (Fig 4.2b).

First, to test if rotated exposure training induces changes in hand localization, we fit an LME to the localization errors throughout the workspace using *session* (aligned or rotated), *movement type* (active and passive) and *hand angle* (25°, 35°, 45°, 55°, 65° and 75°), and all interactions as fixed effects and *participant* as random effect. There was an effect of *session* (F(1,450.5)=155.8; p<0.001), showing that exposure training leads to changes in hand localization. There was also an effect of *hand angle* (F(5,450.6)=6.54; p<.001) and an interaction between *hand angle* and *session* (F(5,450.3)=8.25; p<.001), but no other effects (all p>.60), which we’ll explore below. Since localization responses shifted, for further tests we use the difference between hand localization after rotated training and after aligned training (as plotted in Fig 4.2).

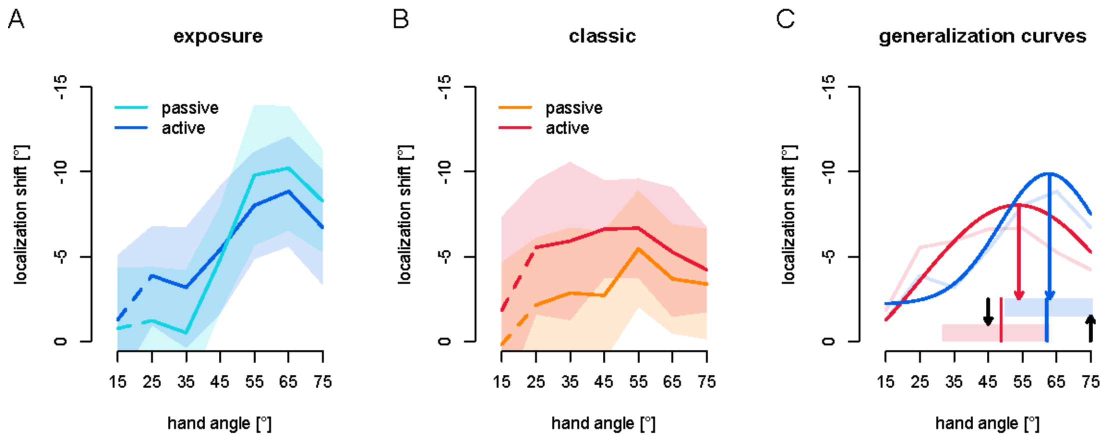

Figure 4.2 The shifts of the angles of touchscreen responses in all variations of the localization task, using spline-interpolated estimates for hand angles matching the reach targets in the no-cursor reach block. **a)** Localization shifts after exporure training. Dark blue: active localization shifts, Light blue: passive localization shifts. **b)** Localization shifts after classic training. Dark red: active localization shifts, Orange: passive localization shifts. The dashed line segments illustrate that the 15° data is not used for statistical analyses (see Methods). **c)** Generalization curves of active localization shifts after exposure training (blue) and classic training (red). Shaded areas: 95% confidence intervals for the peak of the generalization curve (red and blue lines through shaded area indicate 50% points). Downward black arrow: visual trained target. Upward black arrow: hand location during training.

If this shift in localization after exposure training partly reflects predicted sensory consequences, then shifts in active localization, that rely on both (recalibrated) proprioception and (updated) predictions should be different from shifts in passive localization that only rely on (recalibrated) proprioception. We fit an LME to the change in localization using *movement type* (active or passive localization) and *hand angle*, as well as their interaction as fixed effects and *participant* as random effect. There was no effect of *movement type* (F(1,211.8)=0.07; p=0.79). There was an effect of *hand angle* (F(5,212.2)=10.8; p<0.001), but no interaction between *hand angle* and *movement type* (F(5,211.8)=1.23, p=.29). The lack of an effect of *movement type* suggests that predicted sensory consequences did not contribute to localization in this paradigm.

In order to compare hand localization shifts after exposure training with those after classic training ('t Hart & Henriques, 2016), we fit an LME to localization shift using *training type* (exposure vs. classic), *movement type* (active vs. passive) and *hand angle* and all interactions as fixed effects and *participant* as random effect. There was a main effect of *movement type* (F(1,422.0)=6.22; p=.013) and of *hand angle* (F(5,422.7)=8.19; p<.001), as well as an interaction between *training type* and *hand angle* (F(5,422.7)=4.54; p<.001) and between *training type* and *movement type* (F(1,422.0)=4.48, p=.035), but there was no main effect of *training type* (F(1,39.1)=0.92, p=.34) and no other effects (all p>.14). These results also suggests that the magnitude of the shifts in localization are comparable between classic and exposure training, but that the pattern of generalization is different.

To address our main question, we will look at the interaction between *training type* (exposure vs. classic) and *movement type* (active vs. passive) we found above. Since there is no difference between active and passive localization shifts after exposure training alone, the interaction between *training type* and *movement type* should be caused by an effect of *movement type* on the localization shifts after classic training, as we found previously ('t Hart & Henriques, 2016). This means that shifts in hand localization after exposure training indeed relies on recalibrated proprioception alone, while after classic training, there also is a contribution of predicted sensory consequences to active localization.

For completeness, we explore the potentially different generalization patterns of localization shifts after classic and exposure training (Fig 2c). The LME indicates no difference in overall amplitude of localization shifts between the groups, so the interaction between *training type* and *hand angle* might stem from a generalization that does not peak at the trained location after exposure training. Using the active localization shifts only (which are larger, and arguably more similar to reach aftereffects), we bootstrap a 95% confidence interval for the peak localization shift across participants in each group. Here we include the data at 15° where it is available. After classic training, the peak localization shift was at 48.7° (95% confidence: 31.6° -

62.8°; red area in Fig 2c), and after exposure training the peak localization shift was at 62.1° (95% confidence: 50.0° - 75.6°; blue are in Fig 4.2c). This means that peak localization after classic training is lower than after exposure training, but not vice versa. Also note that the confidence interval for the peak localization shift after classic training includes the trained target (45°), but not after exposure training (Izawa et al., 2012). In short, the LME for localization shifts indicates a different generalization curve after exposure and classic training, which could be partially explained by a different position of the peak localization shift after exposure or classic training.

4.5.2 Reach aftereffects

Apart from proprioception and prediction, we want to see if rotated exposure training has any effect on open-loop reaches and if these are robust. We measure whether participants adapted their reach directions by assessing their reach errors in no-cursor reach trials after aligned and rotated exposure training. In Fig 4.3, the changes in no-cursor endpoint errors, or reach aftereffects, appear to be well over 5°. First, to test if exposure training affects open-loop reach direction, we fit a linear mixed effects model (LME) to reach endpoint error using *session* (aligned; all blocks, or rotated; only the first block immediately after training) and *target* (15°, 25°, 35°, 45°, 55°, 65° and 75°), as well as their interactions as fixed effects and *participant* as random effect. There is an effect of *session* (F(1,260)=93.81, p<.001), that is: exposure training leads to substantial reach aftereffects. There was no effect of *target* (F(6,260)=1.07, p=.37) and no interaction (F(6,260)=1.00, p=.42). Since there is an effect of *session*, we now take the differences in reach endpoint errors between the rotated and aligned session for every participant and target as reach aftereffects, and use those for all further analyses.

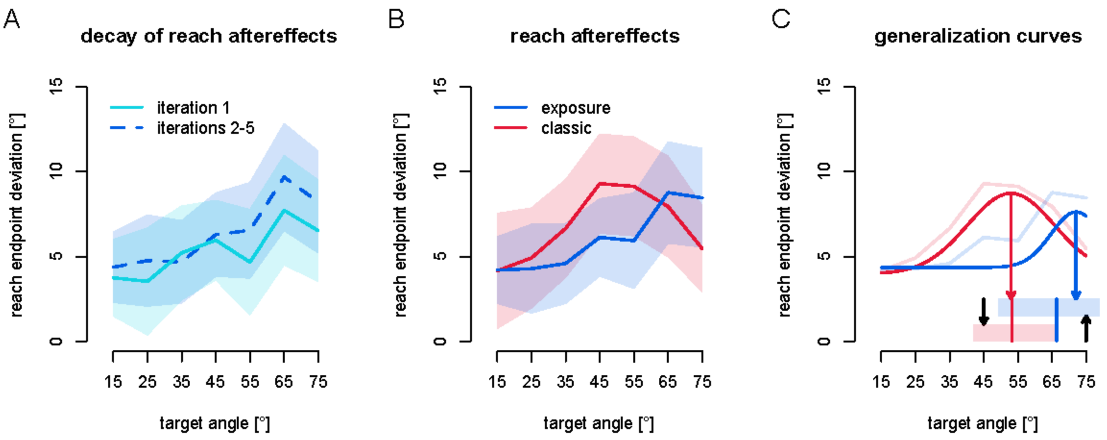

Figure 4.3 Changes of the angle of reach endpoints in the no-cursor tasks. a) Reach aftereffects across the experiment. Light blue: first no-cursor task in the rotated session (immediately following training), Dark blue, dashed line: he other four repetitions of the task (with localization in between training and no-cursor tasks). b) Reach aftereffects after classic and exposure training. Blue: exposure training, Red: classic training. c) Generalization curves of reach aftereffects after exposure training (blue) and classic training (red). Shaded areas: 95% confidence intervals for the peak of the generalization curve (red and blue lines through shaded area indicate 50% points). Downward black arrow: visual trained target. Upward black arrow: hand location during training.

To see if reach aftereffects decayed during the localization tasks, we compared reach aftereffects in the initial no-cursor block, that immediately followed training, with those in the later blocks that followed a localization task. We fit an LME to the reach aftereffects with *iteration* (initial vs. later no-cursor blocks) and *target* (as above) as well as their interaction as fixed effects and *participant* as random effect. There is no effect of *iteration* (F(1,260)=2.72, p=0.10). There was an effect of *target* (F(6,260)=6.29, p<.001) but no interaction (F(6,260)=0.58, p=0.74). Hence, reach aftereffects were not appreciably different right after training and after the localization tasks. In other words, there was likely no noticeable decay of reach aftereffects during the localization tasks, so that we can collapse the data across iterations.

Now we compare the reach aftereffects after classic training with those after exposure training (Fig 4.3b). It appears as if there is little overall difference in magnitude, but there might be a shift of the generalization curve. We fit an LME to reach aftereffects with *training type* (classic vs. exposure), *target* (as above) as well as their interaction as fixed effects and *participant* as random effect. There is no main effect of *training* (F(1,40)=0.11, p=.74) indicating approximately equal magnitude of reach aftereffects after the two training types. There is an effect of *target* (F(6,240)=8.36, p<.001), indicating that reach aftereffects exhibit some form of a generalization curve. There is also an interaction between *training type* and *target* (F(6,240)=2.27, p=.038), indicating these generalization curves are different after the two training types.

We will explore these potentially different generalization curves here. In Fig 4.3c we can observe that reach aftereffects after exposure training seem not to peak at the trained target direction of 45° but a more forward direction. We test this by taking the 95% confidence interval of the centre of a normal curve fit to this data, bootstrapped across participants, and find that the median peak of the generalization curve of reach aftereffects after exposure training is at 66.3°, with a 95% confidence interval ranging from 49.3° to 78.9° this would indeed suggest that the reach aftereffects after exposure training do not generalize around the trained direction of 45°, but at a more counter clockwise location. For classic training, generalization of reach aftereffects peaks at 53.2°, with a 95% confidence interval spanning 42.0° to 66.4°. So for classic training the 95% confidence interval for peak reach aftereffects does include the trained target. These confidence intervals also indicates that generalization of reach aftereffects does not peak at different target position after exposure and classic training. However, we can also observe that the full curve was not sampled after exposure training, so that curve fitting is not optimal. This means that – given our data – the interaction between *target* and *training type* found in the LME above can't be explained by a shifted generalization curve.

In summary, our main hypotheses are confirmed; exposure training leads to shifts in hand localization that are not different for active or passive localizatoin, while movement type does have an effect on localization shift after classic training. Exposure training also causes robust reach aftereffects that are of comparable size to those found with classic training. There is some evidence that the generalization of both localization shifts and reach aftereffects are different after the two training types, and it appears this can partially be explained by a different peak of the generalization curves, but our data and analyses are not definitive.

4.6 Discussion

The position of limbs is important for planning and evaluating movements, and can be estimated through predicted sensory consequences, as well as visual and proprioceptive feedback. As in a previous study ('t Hart & Henriques, 2016) here we quantify the contributions of predicted sensory consequences and proprioceptive recalibration to where we localize our hand after training with altered visual feedback of the hand. In classical adaptation paradigms, both predictions are updated and proprioception is recalibrated. Predictions are updated when they don't match actual sensory consequences, and proprioception is recalibrated when it doesn't match visual feedback. In this study we use "exposure" training, where the participants do not have volitional control of their movements. By design. this should eliminate efference copies and prevent updating predicted consequences of movements, but since the proprioceptive and visual feedback is the same, exposure training still allows proprioceptive recalibration. Before and after training, participants localize their hand, both after "active," self-generated movements that allow using predicted sensory consequences, and after "passive," robot-generated movements that only allow using proprioception. We calculate the training-induced shift in both types of localization given the same actual hand position. After classic training we previously reported larger shifts in active localization as compared to passive ('t Hart & Henriques, 2016). As we expected, after exposure training there are substantial shifts in localization, but no difference between active and passive localization, indicating that predictions are not updated after exposure training. Furthermore, we find that exposure training evokes substantial and robust reach aftereffects, indicating that recalibrated proprioception is used to plan movements.

Our lab previously investigated proprioceptive recalibration and reach aftereffects following visuomotor adaptation with classic training and matched exposure training. There we also found that proprioceptive recalibration is of similar magnitude in both training paradigms, but unlike here, reach aftereffects are usually much larger with classic training (Cressman & Henriques, 2010; Henriques & Cressman, 2012; Henriques et al., 2014; Ruttle et al., 2018; Salomonczyk et al., 2013). And while proprioceptive recalibration and reach aftereffects do proportionally increase with gradual increases in rotation size for classical training, they do not for exposure training (Salomonczyk et al., 2013). The similar magnitude of proprioceptive recalibration and reach aftereffects following exposure training, but not classical training, suggest that this sensory recalibration is partly driving this modest change in movements. The effect of exposure training on movements is also demonstrated by savings and interference from exposure training to subsequent classic training (Sakamoto & Kondo, 2015) and transfer of exposure training effects from one hand to the other (Bao, Lei, & Wang, 2017). In the current study, we further demonstrate that exposure training affects movements and proprioception, but also measure its potential effect on predictive estimates.

Results similar to what we find here were reported in a study by Cameron and colleagues (Cameron et al., 2012), using gain modulation of visual feedback of single-joint hand movements around the elbow. Their within-subjects experiment included both training with volitional movements as well as with passive movements and also tested perception of movements that were either passive or active. They too found a robust change in passive perception of hand movement (using a different measure), and these changes did not differ between the two types of training. Similarly, they found shifts in what we might call “active localization,” although the task is different, after both training types. Like here, these shifts are larger after classic training as compared to exposure training. They also found that passive exposure leads to reach aftereffects, although these were smaller than those produced following “classical” training with altered visual gain. Both our findings, and those of Cameron et al. (Cameron et al., 2012) indicate that updating predicted sensory consequences requires volitionally controlled movements that lead to prediction errors, while proprioception recalibrates equally in both types of training, and that recalibrated proprioception affects open-loop reaches. Our combined results suggest that updates in predicted sensory consequences only provide a partial explanation for motor learning.

In our classical training group, we not only see shifts for passive localization but even larger shifts for active localization which is consistent with a change in both proprioception and an update in predictions. In our exposure training, we did not find a consistent difference between active and passive localization, and none at the trained direction. Assuming that predictions were not updated in exposure training, a maximum likelihood estimate (MLE) or “optimal integration” (Ernst & Banks, 2002) would predict that active localization should shift less than passive localization after exposure training. But of course this is not the case in our findings (although it is the case for Cameron et al., 2012). This suggests that perhaps these two signals are not optimally integrated which is consistent with our comparisons of the variance between passive and active localization. In ’t Hart and Henriques (’t Hart & Henriques, 2016), we tested the prediction derived from MLE that hand localization with two signals – proprioception and prediction in active localization – should be more reliable, i.e., have lower variance, than hand localization with only one signal – proprioception only in passive localization. However, we found no difference in variance between active and passive localization, and recently replicated this in a much larger dataset (’t Hart, Ayala, & Henriques, 2018). Taken together, this suggests these different sources of information about unseen hand location are not optimally integrated. While localizing the unseen hand is less precise than locating (pointing to) a remembered visual target or a seen and felt hand location, we find that these bimodal estimates are rarely integrated optimally (Byrne & Henriques, 2013; Fiehler, Rösler, & Henriques, 2010; Jones & Henriques, 2010), although others have (Beers, 2002). A more recent study (Mikula, Gaveau, Pisella, Khan, & Blohm, 2018) has also shed doubt on whether “optimal” or “Bayesian” integration is used for locating the hand with two afferent signals. Analogously, here we again can’t find evidence that afferent and efferent information combine as a maximum likelihood estimate.

It seems clear that the cerebellum plays a role in motor learning as it appears to compute predicted sensory consequences, i.e., it implements a forward model. (Bastian, 2006; Shadmehr & Krakauer, 2008; Wolpert, Miall, & Kawato, 1998) People with cerebellar damage do worse on motor learning tasks (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010; Donchin et al., 2012; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Maschke, Gomez, Ebner, & Konczak, 2004), and show decreased shifts in hand localization tasks following motor learning (Izawa et al., 2012; Synofzik et al., 2008). This highlights that the cerebellum, and likely predicted sensory consequences, are important for motor learning, but does not explain the remaining shifts in hand localization. We previously found that proprioceptive recalibration is intact in people with mild cerebellar ataxia and that it is similar following exposure and classical training with a gradually introduced cursor rotation (Henriques et al., 2014). The remaining changes in hand localization found in cerebellar patients can be attributed to recalibrated proprioception which should be intact (Henriques et al., 2014). Analogously, here we show that in a paradigm that stops updates of predictions of sensory consequences, as supposedly in people with cerebellar damage, we still see substantial shifts in localization. Again, the remaining localization shifts can be explained if, along with predictions, we use afferent recalibrated proprioceptive estimates to localize our hand.

4.6.1 Generalization

We do find some evidence that, after exposure training, the generalization curves for localization shifts are not centred on the visual location of the trained target; they don’t peak at 45° but at ~62°. In contrast, after classic training the peak of the generalization curve does peak close to the training target. It is possible that proprioceptive recalibration is not anchored to the visual goal of the training task as it is not a requirement to feel your hand at any specific point; rather the visual cursor has to be brought to a visual target to end a trial. Although we can’t substantiate this here, the generalization curves of the reach aftereffects seem to mimic the generalization curves of localization shifts, suggesting a relationship between changes in state estimates and changes in movements. This needs to be tested further, but if these effects are true, they may provide insight into how state estimates are used to produce movements, and also may lead to a way method to disentangle the influence of recalibrated proprioception and more traditional updated internal models on motor changes, such as reach aftereffects. Either way, even though the experiment was not designed to investigate this, the shifted generalization curves of changes in localization after classic and exposure training suggest they are generated by different mechanisms. This is in line with our earlier findings that proprioception generalizes differently from reach adaptation (Mostafa et al., 2015; Mostafa, Kamran-Disfani, Bahari-Kashani, Cressman, & Henriques, 2014).

4.7 Conclusion

To sum up, after a training paradigm designed to prevent updating of predicted sensory consequences but allow recalibration of proprioception, we find substantial changes in where people localize their hand. This means that recalibrated proprioceptive estimates can explain shifts in localization. Since our participants also changed the direction of open loop reaches, recalibrated proprioception seems to guide motor planning. Finally, we have some evidence that after exposure training, the shift in hand localization does not generalize around the trained target location, confirming that different mechanisms underly proprioceptive recalibration and motor adaptation.

CHAPTER FIVE

GENERAL DISCUSSION

In this dissertation we aimed to characterize proprioceptive recalibration process that occurs as a result of exposure to visuomotor error signals and/or visual-proprioceptive error signals. Following training with a translated cursor, we found that proprioceptive recalibration is specific to the trained hand and does not transfer intermanually, unlike reach adaptation. However, proprioceptive recalibration does generalize across different distances in the workspace similar to reach adaptation, although generalization of proprioceptive recalibration is significantly smaller for farther distances. Moreover, mere exposure to visual-proprioceptive discrepancy results in proprioceptive recalibration that was observable across the workspace despite of how participants' hand moved in our hand localization tasks.

Characterizing generalization across different domains provides insight into what exactly the brain is adapting to when adaptation is required to achieve a movement goal. Specifically, the sources of the errors that need to be corrected, as well as, the reference frames used for coding and remapping movements.

5.1 Intermanual generalization

In Chapter two, motor adaptation was observed to the same extent in both the left and right trained hand, however, these motor changes did not symmetrically transfer to the opposite untrained hands. We found significant reach aftereffects for the untrained left hand following training with the right hand, no transfer of reach aftereffects was observed in the untrained right hand following left hand training. Previous findings from our laboratory (Salomonczyk, Cressman, & Henriques, 2010), in which a different distortion was employed, found similar result, that is, intermanual transfer only occurred after right-hand adaptation and only the untrained left hand produced significant reach aftereffects. In the current study we introduced a lateral translation instead of rotation to allow for greater generalization effects as it has been suggested in the literature (Ghahramani et al. (1996); Krakauer et al. 2000). Nonetheless, these results suggest the asymmetry in transfer is not due to the type of distortion (i.e., translated or rotated cursor), as it occurred in both cases. Additionally, following adaptation to displacing prisms Redding and Wallace (2008) have found asymmetric transfer consistent with our findings. Moreover, using a force filed training paradigm, similar findings were reported by other laboratories (e.g., Criscimagna-Hemminger et al., 2003; Galea et al., 2007). The asymmetric transfer between the right and left trained hands is due to symmetrically lateralized limb control but asymmetrical spatial mapping, where the right limb is represented in both hemispheres, while the left limb is represented only in the right hemisphere. Our findings are consistent with the "cross-activation model" proposal which posits that only training with the dominant hand stores a weaker copy of memory in the non-dominant hand hemisphere which influences the non-dominant hand performance.

Transferred motor changes usually are a proportion of the motor changes in the trained hand, no study we know of have found complete intermanual transfer. According to credit assignment model, the CNS estimates the source of motor errors and assigns these errors to changes in the environment or in the body (Berniker and Kording, 2008). This assignment determines how the CNS should generalize motor correction or adaptation across different body parts or workspace. For example, if participants believe that motor errors are driven by an injury in their right hand, then they should not transfer motor adaptation to the other hand. In a recent study Kong et al. (2017) examined how learning transfer in a weight-transportation task. They looked at transfer of learning when using the opposite hand with the same object, or the same hand with an second but identical object, or with the opposite hand and the second identical object. They found that participants attribute 25% of motor learning to a manipulated object and attribute 58% of motor learning to their own body. This means that partial motor intermanual transfer, in our study, could be a result of a higher attribution of motor errors to the trained hand.

In Chapter two, we also found that participants' felt hand position has been shifted in both left and right hand for the hand that was exposed to the translated visual feedback; however, no significant transfer between the two hands occurred. We assessed changes in hand proprioception using a perceptual task that did not require any goal-directed movements of the assessed hand. The task was designed by Cressman and Henriques (2009) to measure proprioceptive changes in isolation from motor changes by removing the motor component from the task. Similar lack of proprioceptive recalibration transfer between hands has been found by Salomonczyk et al. (2010) they introduced a 30° rotation to two groups (i.e., left- and right-hand training), they found that participants were able to recalibrate their hand proprioception equivalently in both groups, while the mean biases in one hand remained unchanged following opposite-hand training. This suggests that proprioceptive recalibration is specific to the trained hand and does not transfer to the opposite untrained hand.

The lack of proprioceptive transfer despite a small but significant transfer for the movements may have to due to the nature of the signals driving sensory and motor changes. As described in Chapter 4 and in earlier work from our lab, the main signal driving proprioceptive changes (and only a portion of reach changes) is the discrepancy between vision and proprioception, what we call cross-sensory error signals (i.e., visual-proprioceptive discrepancy, see Chapter four in this dissertation). This conclusion is based on evidence showing that the magnitude of proprioceptive recalibration is the same when training with both visuomotor and visual-proprioceptive error signals, although reach aftereffects are much larger following visuomotor training. In their review article Cressman and Henriques (2012) have suggested that like credit assignment model, a similar model could also account for independent changes in hand proprioception based on different error signals. Accordingly, if the CNS attributes cross-sensory errors mainly to the hand and attributes visuomotor errors more to the environment, then proprioceptive recalibration should not transfer to the opposite untrained hand. This is consistent with our results.

Likewise, partial transfer of motor adaptation might point at a missing component that does not transfer between hands, in this case is proprioceptive recalibration. Participants performance in open-loop reaching tasks (which are used to examine reach adaptation/transfer) following training reflect both changes in visuomotor map and changes in hand proprioception. In the current study, we found that the magnitude of proprioceptive recalibration when measured alone is around 50% of reach aftereffects and the magnitude of transferred reach aftereffects to the opposite hand is approximately 30% of reach aftereffects. Thus the missing proportion of transferred reach aftereffects reflects non-transferable component that is proprioceptive recalibration. This might suggest that since proprioceptive changes do not transfer between hands, partial interlimb transfer of motor adaptation occur.

5.2 Workspace generalization

Generalization of adaptation has been extensively explored across different directions and amplitudes across the workspace. Several studies, including ours suggest that the extent and pattern of generalization for reach adaptation varies with the direction and the distance of the novel target (relative to the trained location) in the workspace. Our study in Chapter three is one of the first to explore generalization pattern for proprioceptive recalibration.

Generalization is almost complete for novel targets that differ from the trained distance. This is illustrated by our results in Chapter three, where we found that reach adaptation generalized to a similar extent (i.e., similar size reach aftereffects) to novel movement distances (novel-near, and novel-far targets) compared to trained distance/location. This is consistent with previous findings, for example, Krakauer et al. (2000) and Shabbott and Sainburg (2010) found that reach adaptation following visuomotor rotation training to a single target was fully generalized to novel targets in the same direction but at different distances, with novel target distances that were up to 50% farther than the trained distance. Likewise, Goodbody and Wolpert (1998) found that reach adaptation to a velocity-dependent forced field completely generalized to novel targets that were twice as far, relative to the trained target, although Matter and Ostry (2010) found that the farther targets (also twice of the distance of the trained target) lead to only partial generalization of force field adaptation. Although it is unknown the extent by which generalization transfer to greater distances, it is almost complete for distance within 50% of trained target distance.

This generalization pattern of reach adaptation appears to modulate more across directions than across distances. The generalization pattern, whether for visuomotor or force field adaptation, tends to be more restricted to the trained direction, tapers off as the deviation between training and novel target increases in a gaussian manner (Cressman & Henriques, 2015; Krakauer et al., 2000; Pine et al., 1996) However, this generalization-pattern tends to be maintained for the same movement directions but from a different start location (Cressman & Henriques, 2015; Wang & Sainburg, 2005). These results suggest the hand-centered reference axes or reach direction are being remapped during visuomotor rotation training.

There are a couple explanations or mechanisms to explain the broad generalization pattern seen when reaching to different distances of the workspace compared to the more limited generalization that is produced when testing novel directions. One possible distinction is how direction and amplitude are coded neurally (Georgopoulos, Kalaska, Caminiti, & Massey, 1982). The Gaussian pattern of generalization across novel directions resembles the Gaussian pattern of tuning curves of sensorimotor neurons, and there is some evidence that the peak of the tuning curves for some primary motor neurons shift following force field adaptation (Li, Padoa-Schioppa, & Bizzi, 2001) and for visuomotor adaptation (Paz, Boraud, Natan, Bergman, & Vaadia, 2003). In contrast, the turning of neural activity or the neural populations is less clear as a function of distance, and likely involves a modulation of the firing rate (Fu, Suarez, & Ebner, 1993). The weaker, or perhaps broader, tuning for movement amplitude may in turn explain greater generalization across different movement amplitude. On the muscular level, another explanation could be that when testing generalization to different amplitudes participants are activating same muscle groups of which they use during adaptation, this results in complete generalization, compared with generalization to locations that require recruiting different muscles (de Rugy, 2010). Thus the neural and muscular recruitment involved in both trained and novel targets may explain distinctions in the pattern of generalization across the workspace, and likewise the limited generalization across the two arms.

Generalization of proprioceptive recalibration has been largely unexplored. Like in Chapter two, in Chapter three we examined the generalization pattern of proprioceptive recalibration, but across different distances. We found that proprioceptive recalibration occurred at the training target and generalized across novel locations at different distances of the workspace; however, the extent of generalization depends on the distances of the novel tested location related to the trained location. That is proprioceptive recalibration at far-novel targets was 40% smaller, compared to near-novel and training targets. Considering these findings we suggest a distance-dependent generalization for proprioceptive recalibration, due to the fact that the participants (in the training tasks) have had experience with the visual–proprioceptive discrepancy of novel-near locations while reaching to the training locations. This may have influenced participants' estimates at the novel-near locations more than for the novel-far locations where no such sensory discrepancy was experienced. In contrast, reach adaptation has generalized equivalently for near and far targets, where change in motor commands plays a greater role in adaptation.

Unlike for distances, the pattern of generalization of proprioceptive recalibration tended to transfer even to directions farther than trained direction. Cressman and Henriques (2015) showed that hand proprioception was recalibrated by a similar amount both for trained and novel directions that deviated from the trained direction by 45 and 90 degrees. As we mentioned above, the sensory changes, found in our study, were significantly smaller for the novel-far compared to the trained distance. The difference between generalization patterns for proprioceptive recalibration across the two studies suggests that proprioceptive information regarding the extent and direction of the hand movement may be processed differently in the brain.

Likewise, the pattern of changes across novel movements also differed when the novel movements varied in distance or direction relative to the trained location. In the present study, reach aftereffects 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 (2015) showed that generalization of reach adaptation was limited to the trained direction, and decreased as novel targets deviated in the direction of training. The generalization patterns for proprioceptive recalibration differed from reach adaptation in both studies. These results provide further evidence in support of the proposal that proprioceptive recalibration may arise independently of changes in the motor system.

These small differences between proprioceptive recalibration across distance and direction may be due to differences in the precision of visual and proprioceptive processing across these two axes. Precision of these sensory inputs will affect how much the brain relies on (or weights) each when both sources are available. This may be particularly true when the sensory inputs are in conflict like for when a visuomotor distortion is introduced (van Beers, Wolpert, & Haggard, 2002). In most cases vision dominates proprioception, but this greater weight on vision tends to be larger in azimuth direction where visual precision is greater (van Beers et al., (2002). But in the depth direction, hand proprioception is more precise and the relative weight for proprioception is greater. It's possible that when hand location is tested away from the trained location in depth, the estimate of the unseen hand will rely less on prior visual training. This should be less the case when hand location varies along its less-precise azimuth axis. This may explain our results and why visual recalibration of hand proprioception varies somewhat with the direction and distance from the trained location.

5.3 Visual-proprioceptive discrepancy and hand localization

It is unclear how proprioception, vision and sensory predictions contribute to reach adaptation. Deafferented patients adapt their reaches with visual feedback, suggesting that proprioception is not absolutely necessary for reach adaptation (Miall et al., 2018).While healthy participants can adapt to imposed forces without or with visual feedback of their hand, which may suggest that proprioception is sufficient for reach adaptation (Miall et al., 2018). Cerebellar patients also adapt their reaches even without being able to update visual predictions of their hand reaches (Izawa et al., 2012). In Chapter four, we exposed healthy right-handed participants to a visual-proprioceptive mismatch by having a robot gradually deviate the hand motion away from the hand-cursor that moved directly to the target. This passive-training paradigm allows us to remove the motor component during the training task in order to isolate efference-based predictions and understand the contribution of the visual-proprioceptive discrepancy alone to changes in motor and sensory recalibration.

How people adapt their reaches following the visual-proprioceptive discrepancy (or cross-sensory error signals) training has been examined previously (Cressman & Henriques, 2010). The authors found that following exposure to the cross-sensory discrepancy, subjects estimated their hand position to be shifted in the direction of the distortion, and roughly by the same amount as produced following classical visuomotor adaptation (Cressman & Henriques, 2009). Moreover, this passive sensory training also led to reach aftereffects, although these motor changes were smaller than those produced by classic visuomotor distortion training. In Cressman and Henriques (2010) study reach aftereffects were significantly correlated with proprioceptive recalibration and were about the same size. The authors suggested that the sensory and motor systems are influenced by mere exposure to the sensory-discrepancy between vision and proprioception. This discrepancy also partly contributes to the motor and sensory changes that occur during classic visuomotor distortion training, which includes visual-proprioceptive mismatch in addition to the visuomotor mismatches. Some follow-up studies have shown that these sensory and motor changes emerge within just 6 trials of visual-proprioceptive discrepancy training (Ruttle, ‘t Hart, & Henriques, 2018), as well as in classic visuomotor training (Ruttle et al., 2016). But, unlike following classic visuomotor training, these sensory and motor changes do not increase with further increases in visual and proprioceptive discrepancy, in that, these changes tend to saturate at same degree following training with different magnitudes of the visuomotor distortion 30°,50° and 70° (Salomonczyk, Cressman, & Henriques, 2013). Although partly addressed in the Cameron et al. (2012) described below, how this visual-proprioceptive discrepancy training affects sensory prediction is still unknown.

In Chapter four, both before and after this visual-proprioceptive discrepancy training, we measured resulting changes in volitional reach movements (open-loop reaches) and estimates of hand location. The localization tasks used to measure these hand estimates involved either after the hand was moved by a robot (passive localization) or self-generated by the participant (active localization). This allowed us to determine the extent of predicted (efferent-based) sensory consequences and proprioceptive recalibration changes following visual-proprioceptive discrepancy training. We hypothesized that following exposure training we will find no differences between shifts in active and passive hand localization, because no volitional reaches in training means no efference-based signals and in turn no updated predictions. Thus, any shifts in hand localization should reflect proprioceptive recalibration only and not updated predictions. We found that exposure training induced both substantial and robust reach aftereffects and shifts in hand localization. More importantly, as predicted, we found no difference in unseen hand estimates between active and passive conditions. Given that active localization should reflect both proprioceptive changes and efference-based updated predictions, whereas passive localization reflect only changes in hand estimates (because no efference-based signal is available), no differences between the two conditions confirms that efference-based predictions were not updated following exposure to visual-proprioceptive discrepancy alone. This suggests that updated predictions are not the only mechanism for motor adaptation and hand proprioception plays a main role in adaptation process.

A few labs have shown that forward models deficits affect hand localization, patients with damage in the cerebellum (where forward models takes place) could not update sensory predictions of hand location as normal controls could (Izawa et al., 2012; Synofzik et al., 2008; Weeks, Therrien, & Bastian, 2016). In Izawa et al., (2012) and Synofzik et al., (2008) experiments, following training with rotated visual feedback, participants with cerebellar damage and healthy participants made reaches with their right (unseen) hand and then indicated its location. They found that shifts in hand localization were significant between the two groups the authors explained this as an evidence that predicted sensory consequences are updated as a result of visuomotor rotation adaptation. However, cerebellar patients did still show some change in hand estimates which may reflect proprioceptive recalibration. To investigate this, using a 2AFC perceptual task similar to that used in Chapters 2 and 3, Henriques et al., (2014) measured proprioceptive recalibration in participants with cerebellar damage and healthy controls. They found similar size of changes in their estimate of unseen hand location compared with intact controls, following both exposure and classic visuomotor training. The authors suggest that the differences between results of their study and those of Izawa et al. (2012) and Synofzik et al. (2008) has to do with the extent by which the change in perceived hand position following adaptation reflect proprioceptive recalibration or updates in predictions. The study designed by Henriques et al. (2014) was meant to isolate only the proprioceptive changes, where the other studies could not differentiate between proprioceptive changes and changes in sensory predictions. Recently, our lab have shown that visual adaptation leads to both updated predictive and perceptual estimates of the hand (‘t Hart & Henriques, 2016). They did so by using not only the same hand localization task (used by Izawa et al., 2012; Synofzik et al., 2008 and by us in Chapter 4) but also by including a second passive version of hand localization task that only reflect felt hand position. This additional passive (robot-generated) localization task ensures that any changes in estimate of hand position did not rely on efference-based information, while changes in active (self-generated) task would rely on both sources. Not surprisingly, in both cases, estimates of hand location, whether based on proprioception (in the passive condition) or on both proprioception and prediction (in the active condition), shifted with visuomotor training. And while the changes in hand localization were larger in the self-generated active condition, it was not that much larger than that following passive condition. This suggests that most of the change in hand localization in the active condition could be attributed to solely change in hand proprioception. Specifically, two-thirds of the change in hand localization in the active conditions following adaptation could be attributed to change in hand proprioception, with the remaining third attributable to just updated prediction. In a similar study, Cameron and colleagues (Cameron et al., 2012) examined how participants perceive their hand location following passive or active hand movements. They did so using a gain modulation of visual feedback of single-joint hand movements around the elbow. Their within-subjects experiment included both training with volitional movements as well as with passive movements and also tested perception of movements that were either passive or active. They too found a robust change in passive perception of hand movement (using a different measure), and these changes did not differ between the two types of training. Similarly, they found shifts in what we might call "active localization," although the task is different, after both training types. Like here, these shifts are larger after classic training as compared to exposure training. They also found that passive exposure leads to reach aftereffects, although these were smaller than those produced following "classical" training with altered visual gain. Both our findings, and those of Cameron et al. (Cameron et al., 2012) indicate that updating predicted sensory consequences requires volitionally controlled movements that lead to prediction errors. Additionally, hand proprioception recalibrates equally in both types of training, and that recalibrated proprioception affects open-loop reaches. Our combined results suggest that updates in predicted sensory consequences only provide a partial explanation for motor learning.

Consistent with the previous studies (Cameron et al., 2012; Cressman & Henriques, 2010; Henriques et al., 2014 and this study) using visual-proprioceptive discrepancy training we found significant reach aftereffects, although smaller than those produced following classic visuomotor training. Moreover, they tend to be of the same size and correlate with proprioceptive changes. The reach aftereffects produced after visual-proprioceptive discrepancy training suggest that they largely reflect changes in hand proprioception rather than any real motor recalibration. This in turn, suggests that the reverse is true. Part of the motor changes during visuomotor adaptation, which would also include this sensory discrepancy, is actually driven by proprioceptive recalibration.

5.4 Visual-proprioceptive discrepancy and generalization

In Chapter four we also examined the generalization pattern of motor and sensory changes following exposure training to a single diagonal target. We found that following exposure training, reach aftereffects generalized to neighboring novel targets, however, the generalization curve does not peak at 45° (trained direction). This pattern is different from the usual local pattern of generalization following classical visuomotor training, where the peak of the Gausian generalization function coincide with the trained location (‘t Hart and Henriques (2016) (Cressman & Henriques, 2015; Krakauer et al., 2000; Pine et al., 1996). Our exposure training differ than these studies in that, there were no visuomotor error signals during training because the participant’s hand was passively moving toward the training target. The motor changes generalize across different directions in a way similar to the peak in generalization of hand localization following training, whose shifts are also not centered (shifted counterclockwise) on the trained location as well. This consistent similarly between sensory and motor changes following exposure training suggests that proprioceptive recalibration may partially driving motor changes.

The generalization curve following classic visuomotor adaptation training peaks close to the training direction. It is possible that proprioceptive recalibration is not anchored to the visual goal of the training task as it is not a requirement to feel your hand at any specific point; rather the visual cursor has to be brought to a visual target to end a trial. The shifted generalization curves of changes in localization after classic and exposure training suggest they may be generated by different mechanisms.

5.5 Conclusion

Figure 5.1 summarizes the main results from this dissertation. Proprioceptive recalibration is specific to the trained hand. However, it generalizes across the workspace; although the extent of generalization is distance-dependent. Learning-induced change in hand localization reflect mainly changes in proprioceptive-based estimates of the hand rather than efference-based sensory predictions, and entirely on proprioceptive recalibration when movement is removed from training. Similar pattern of changes in proprioceptive recalibration and reach aftereffects following this passive-exposure training suggest that some of the reach aftereffects which normally produced following classic visuomotor training actually reflect proprioceptive changes. These findings should be taken into consideration when designing motor adaptation/learning paradigms in order to study motor learning, teach a motor skill or designing a movement rehabilitation protocol.

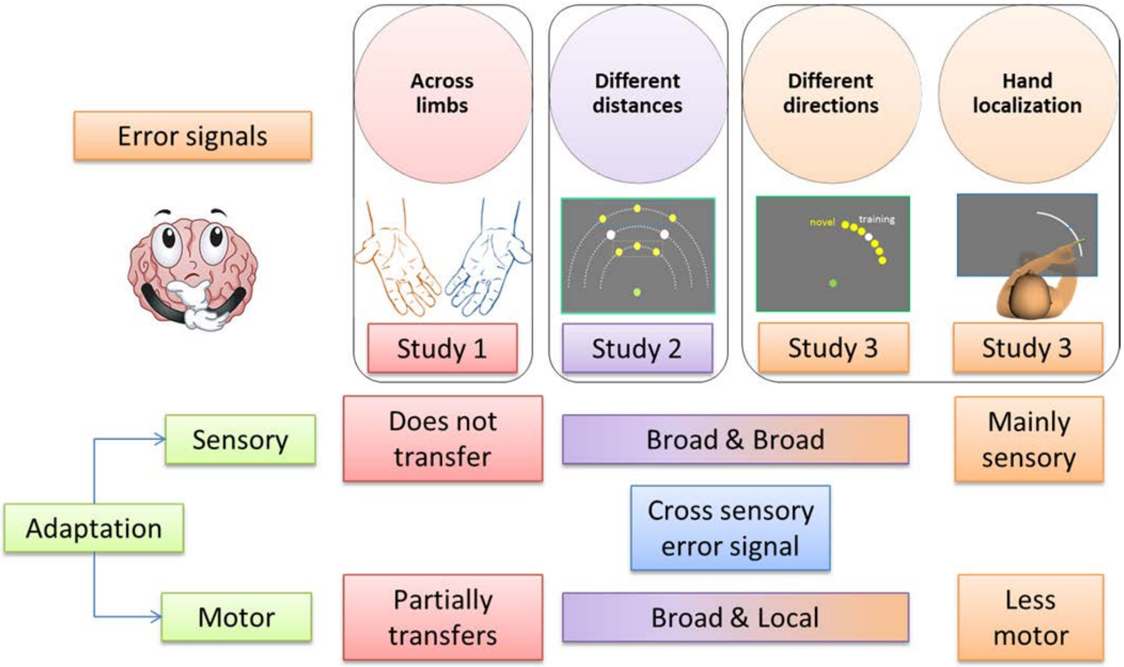

Figure 5.1 Schematic shows our general conclusions. In visuomotor adaptation training, Cross-sensory and sensorimotor error signals result in two distinct processes; i.e., proprioceptive recalibration and reach adaptation. In study one, we found that proprioceptive recalibration does not transfer between the two hands, while motor adaptation partially transfers. Study two shows that both processes generalize broadly across different distances in the workspace. In study three, proprioceptive recalibration shows broader pattern of generalization across different directions, while reach adaptation shows local pattern of generalization. However, following exposure training (when only cross-sensory error signals are available), both processes show broad generalization across directions. Finally, changes in hand localization following visuomotor training reflect mainly proprioceptive recalibration; not efference-based updated sensory predictions.

CHAPTER SIX

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APPENDIX A: AUTHOR CONTRIBUTIONS

Chapter 2:

Mostafa, A. A., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2014). Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand. Experimental Brain Research, 232(6), 1639–1651. https://doi.org/10.1007/s00221-014-3833-0

- Conceived and designed the experiments: Denise Henriques, Erin Cressman, Ahmed Mostafa

- Performed the experiments: Ahmed Mostafa

- Analyzed the data: Ahmed Mostafa (assisted by Danielle Salomonczyk)

- Wrote the paper: Ahmed Mostafa (assisted by Denise Henriques, Erin Cressman, and Danielle Salomonczyk)

***Chapter 3*:**

Mostafa A.A., Kamran-Disfani R., Bahari-Kashani G., Cressman E.K., Henriques D.Y. (2015) Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace. Experimental Brain Research 233: 817–827.

- Conceived and designed the experiments: Denise Henriques, Erin Cressman, Ahmed Mostafa

- Performed the experiments: Ahmed Mostafa (assisted by Roozbeh Kamran-Disfani, Golsa Bahari-Kashani)

- Analyzed the data: Ahmed Mostafa

- Wrote the paper: Ahmed Mostafa (assisted by Denise Henriques, Erin Cressman)

***Chapter 4*:**

Ahmed A. Mostafa, Bernard Marius ’t Hart, Denise Y.P. Henriques (in revision). Motor Learning Without Moving: Proprioceptive and Predictive Hand Localization After Passive Visuoproprioceptive Discrepancy Training. PLoS One.

- Conceived and designed the experiments: Denise Henriques, Bernard Marius ‘t Hart

- Performed the experiments: Ahmed Mostafa (assisted by Shanaathanan Modchalingam)

- Analyzed the data: Bernard Marius ‘t Hart and Ahmed Mostafa

- Wrote the paper: Bernard Marius ‘t Hart and Ahmed Mostafa (assisted by Denise Henriques)

Appendix B: Informed Consent Form (for unpaid participants)

Date:
Study Name: Estimating proprioception following robotic training
Researchers: Dr. _________
Purpose of the Research: Our research team is interested in how people adapt movement of the arm towards visual targets or proprioceptive (felt but unseen hand) target, or estimate of the location or motion of their hand, under various circumstances and using multisensory information.
What You Will Be Asked to Do in the Research: You will be asked to reach or point toward visual targets displayed on a screen and/or point to your unseen other hand (felt target). In most tasks, you will be sitting comfortable in a chair, but some tasks, you will sit in a chair that swivels left and right while you aim your hand to a target.
Risks and Discomforts: We do not foresee any risks or discomfort from your participation in the research.
Benefits of the Research and Benefits to You: You will receive 1.5 credits for participation in this study.
Voluntary Participation: Your participation in the study is completely voluntary and you may choose to stop participating at any time. Your decision not to volunteer will not influence your relationship with us or anyone else at York University either now, or in the future.
Withdrawal from the Study: You can stop participating in the study at any time, for any reason, if you so decide. If you decide to stop participating, you will still be eligible to receive the promised pay for agreeing to be in the project. Your decision to stop participating, or to refuse to answer particular questions, will not affect your relationship with the researchers, York University, or any other group associated with this project. In the event you withdraw from the study, all associated data collected will be immediately removed from our computers.
Confidentiality: All information you supply and recording of your arm movements or judgments about hand location during the experiment will be held in confidence, your name will not appear in any report or publication of the research. Your data will be safely stored password protected computers in our locked laboratory and only research staff will have access to this information. We will keep your information and recording will be destroyed after the study has been published. Confidentiality will be provided to the fullest extent possible by law.

Questions About the Research? If you have questions about the research in general or about your role in the study, please feel free to contact Dr. ______ either by telephone at (xxx) xxx-xxxx, extension xxxxx or by e-mail (______). This research has been reviewed and approved by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, York Research Tower, York University (telephone or e-mail ______).

Legal Rights and Signatures:

I______________________, consent to participate in this study conducted by Dr. Denise Henriques and her research team. I have understood the nature of this project and wish to participate. I am not waiving any of my legal rights by signing this form. My signature below indicates my consent.

Signature__________________________ **Date**________________________
Participant

Signature__________________________ **Date**________________________
Principal Investigator

Appendix C: Published paper references

Exp Brain Res
DOI 10.1007/s00221-014-3833-0

RESEARCH ARTICLE

Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand

**Ahmed A. Mostafa · Danielle Salomonczyk ·
Erin K. Cressman · Denise Y. P. Henriques**

Received: 9 June 2013 / Accepted: 4 January 2014

Abstract Reaching with visual feedback that is misaligned with respect to the actual hand's location leads to changes in reach trajectories (i.e., visuomotor adaptation). Previous studies have also demonstrated that when training to reach with misaligned visual feedback of the hand, the opposite hand also partially adapts, providing evidence of intermanual transfer. Moreover, our laboratory has shown that visuomotor adaptation to a misaligned hand cursor, either translated or rotated relative to the hand, also leads to changes in felt hand position (what we call proprioceptive recalibration), such that subjects' estimate of felt hand position relative to both visual and non-visual reference markers (e.g., body midline) shifts in the direction of the visuomotor distortion. In the present study, we first determined the extent that motor adaptation to a translated cursor leads to transfer to the opposite hand, and whether this transfer differs across the dominant and non-dominant hands. Second, we looked to establish whether changes in hand proprioception that occur with the trained hand following adaptation also transfer to the untrained hand. We found intermanual motor transfer to the left untrained (non-dominant) hand after subjects trained their right (dominant) hand to reach with translated visual feedback of their hand. Motor transfer from the left trained to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike visuomotor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

Keywords Visuomotor adaptation · Proprioception · Sensory recalibration · Intermanual transfer · Reaching · Learning

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Introduction

Moving the hand while its visual feedback is distorted leads to a mismatch of vision and action that results in sensorimotor remapping and adaptation. For example, when subjects first reach to a target with distorted visual feedback (e.g., a cursor that is rotated or translated relative to the hand's actual motion), the cursor reaches are initially deviated but are then gradually adjusted or adapted across trials so that later reaches bring the cursor more directly to the target (Krakauer et al. 1999; Sainburg and Wang 2002; Simani et al. 2007). This visuomotor adaptation has also been shown to transfer across arms, which is referred to as intermanual transfer. In such cases, learning with one hand facilitates subsequent performance with the opposite, untrained hand. Intermanual transfer has been observed in such tasks as drawing (Thut et al. 1996), grasping (Chang et al. 2008), pointing and tracking (Abeele and Bock 2003). More importantly for the current study, intermanual transfer also occurs after adapting reaching movements to displacing prisms (Hamilton and Bossom 1964), force perturbations (Dizio and Lackner 1995), mirror-reversed visual feedback (Dionne and Henriques 2008) and rotated visual feedback of the hand or cursor (Wang and Sainburg 2003, 2004, 2006, 2007; Balitsky Thompson and Henriques 2010). Typically, intermanual transfer of adaptation to these various perturbations is assessed by testing the untrained hand to the same perturbation that the trained hand has adapted to. Transfer is said to occur when initial errors in response to the perturbation are smaller and/or the learning rate is faster for the untrained hand following training of the opposite hand compared to when there is no initial adaptation in the opposite hand.

The pattern of intermanual transfer is not necessary the same across the two hands. In a series of experiments by Sainburg and Wang (2002), they found that when subjects adapted one of their hands to a rotated cursor (visuomotor rotation), the transfer of this learning to the opposite arm was asymmetric, in that the size and types of intermanual transfer depended on the hand trained. Specifically, they found that final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. They proposed that this intermanual transfer pattern reflects basic differences in or specialization of the two arm controllers, such that the initial direction information transferred to the right arm controller from the non-dominant arm; however, the endpoint configuration of the limb, but not the initial direction, transferred to the left arm controller from the dominant arm. In contrast, Balitsky Thompson and Henriques (2010) found intermanual transfer occurred only from the dominant right hand to the left hand, but not from the non-dominant left hand to the right hand, and this was the case when subjects adapted to a rotated cursor or to a rotated video image of the hands (based on angular deviations at peak velocity when the untrained hand reached with the same altered visual feedback). Other motor adaptation studies where subjects adapted to velocity-dependent force fields (Criscimagna-Hemminger et al. (2003), also measuring deviations at peak velocity during training with the previously untrained hand) and displacing prisms (Redding and Wallace (2008), measuring reach endpoint deviations of the opposite arm without the prisms, e.g., aftereffects) have shown a similar asymmetry, training with the dominant hand leads to facilitation with the non-dominant hand.

In the current study, our first goal was to investigate the nature and extent of intermanual transfer after adaptation to a translated cursor. We used a translated cursor (i.e., the cursor appeared rightward of the actual position of the hand and it moved parallel with the hand) as our perturbation rather than the usual rotated cursor (i.e., while the subject moves his/her hand forward, the cursor heads off on a directional angle relative to the hand) since previous results from our laboratory suggest that proportional changes in reaches measured by the resulting aftereffects (relative to the magnitude of the distortion) are greater after adaptation to a translated cursor than to a rotated cursor (Cressman and Henriques 2009). In fact, previous studies by Ghahramani et al. (1996) and Vetter et al. (1999) suggest that adapting to a shifted or translated cursor may also lead to greater generalization across the workspace compared to adapting to a rotated cursor (Krakauer et al. 2000). This difference in both generalization and size of aftereffects following adaptation to a translated cursor compared to a rotated cursor makes sense in that the translated feedback of the hand resembles the kind of visual perturbation one may experience in everyday life, like refracted light from submerging our hand in water, or using a tool that extends or shifts our end-effector. Even a computer mouse resembles a translated shift of the hand more than a rotated shift. In contrast, a rotation perturbation is something we would not experience in everyday life and hence may be more difficult to adapt to. Thus, we used a translated cursor for adapting the hand to provide the greatest possibility of observing intermanual transfer, which is a type of generalization, and one that has not been studied before following translated cursor adaptation. We assessed the extent and pattern of this intermanual transfer of reach adaptation by using a no-cursor (open-loop) reaching task to measure aftereffects of both the trained and untrained hand. We also examined whether this transfer differed across the dominant and non-dominant hands. Given the previous studies mentioned above and those in our laboratory (Balitsky Thompson and Henriques 2010; Salomonczyk et al. 2010) demonstrating that intermanual transfer occurs asymmetrically depending upon the trained hand, in the current study, we hypothesized a similar asymmetry after training with a translated cursor.

In addition to examining intermanual transfer of reach adaptation, we investigated whether changes in felt hand position (i.e., proprioceptive recalibration) also transferred between limbs (what we will call intermanual sensory transfer). Recent studies have shown that visuomotor adaptation leads not only to changes in trajectory of the trained hand, but that the felt position of the hand is also modified (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Ostry et al. 2010; Cressman and Henriques 2011; Salomonczyk et al. 2011, 2012). In our own laboratory, we have found that adapting to either a rotated or translated cursor leads to changes in hand proprioception, such that people perceived their unseen hand as being shifted in the direction of the visual distortion (Cressman and Henriques 2009, 2010). To determine changes in felt hand position, we have subjects estimate the location of their unseen hand relative to a visual or proprioceptive (body midline) reference marker both before and following visuomotor adaptation (Cressman and Henriques 2009, 2010). To date, it has been shown that this proprioceptive recalibration is robust in that it occurs under various task constraints (i.e., adapting to a visuomotor distortion- or velocity-dependent force field) (Cressman and Henriques 2009, 2010; Ostry et al. 2010), regardless of how the hand is displaced during this proprioceptive estimation task (passive arm displacement vs. active reaching movements) (Cressman and Henriques 2009, 2010), the modality of the reference markers (visual vs. proprioceptive) and the age of the patients (young vs. older adults) (Cressman and Henriques 2009, 2010).

Previous studies examining proprioceptive recalibration have focused on assessing shifts in felt right-hand position following motor learning of the right arm in right-handed individuals. It is currently unclear whether, like motor adaptation, such sensory changes transfer to the opposite untrained hand as well. Thus, after establishing the nature and extent of intermanual motor transfer, the second goal of this study was to test whether proprioceptive recalibration transfers from the trained (right or left) hand to the untrained (left or right) hand following adaptation to a visuomotor distortion, and whether this transfer occurs asymmetrically depending upon the hand trained.

Methods

Subjects

In total, 35 right-handed subjects (mean age = 22.9, SD = 5.62, 11 males) were randomly assigned to either the left-hand ($n = 17$) or right-hand ($n = 18$) training groups. All subjects had normal or corrected-to-normal vision. Subjects were prescreened 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 inFig. 1a. Subjects were seated in a chair and the height of the chair was adjusted to ensure that they could easily see all of the targets presented on a reflected screen and comfortably reach to target locations. Subjects were asked to hold on (either with their right or left hand) to the vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA) 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 own hand was blocked by the reflective surface, as well as a black cloth draped over their shoulders.

Procedure

The experiment consisted of 2 test sessions run on 2 separate days. Each test session consisted of 8 tasks (See Fig. 2). The first session had subjects reach to visual targets, after training to reach with a cursor that was *aligned* with either their right or left hand's position. The second session, however, had subjects complete the same reach trials after the right or left hand reached with a cursor that was *misaligned* from their hand's position. The misaligned cursor was translated 4 cm to the right of their actual hand position, with this translation being introduced gradually (as described below).

Aligned reach Training task

The first testing session included aligned reach training (Boxes 1 and 5 in Fig. 2), where subjects were asked to reach to one of five targets with their right or left hand, hidden from view, but represented by a cursor (green circle, 1.4 cm in diameter, Fig. 1b) located above their thumb. In front of the home position, which was approximately 20 cm in front of subjects' chests, there were 5 reach targets represented by 1-cm-diameter yellow circles, located along two lines, 8.66 or 10 cm above the home position. One reach target was located 10 cm directly in front of the home position. Four additional visual reach targets were located 5 and 7.5 cm to the left and right of the center reach target, 8.66 cm in front of the home position. The reach trial was considered complete when the center of the cursor had moved to within 0.5 cm of the target's center. At that point, both the target and cursor were removed 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)]

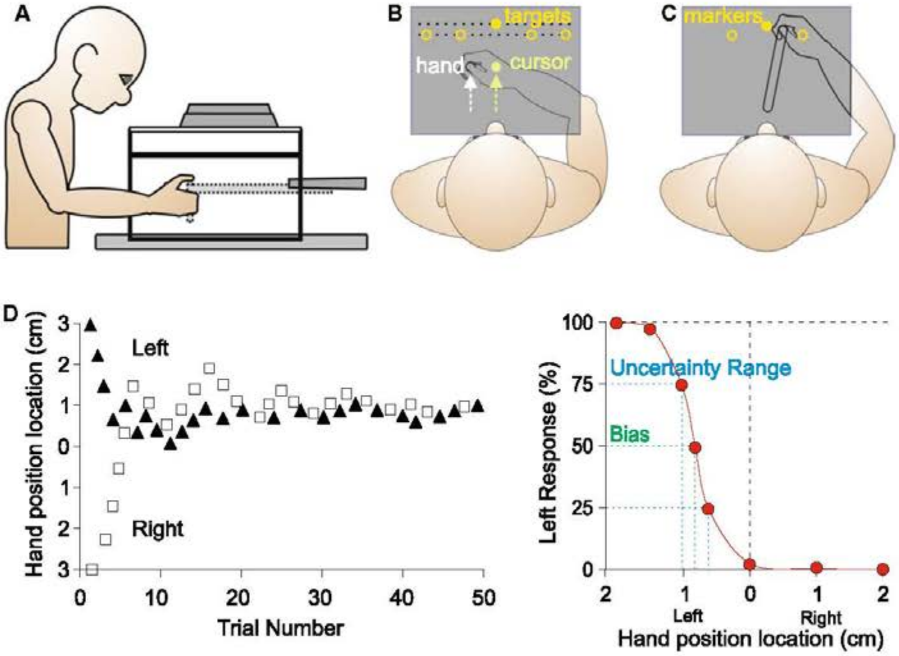

Fig. 1 Experimental setup and design. **a** Side view of the experimental setup. **b** Top view of experimental setup visible to subjects in the reaching tasks. The center home position was represented by a 1-cm *green circle* and was located about 20 cm in front of subjects' chests, aligned with the body midline, this position was not illuminated, and visual feedback was provided only when the hand had travelled 4 cm outwards from the home position. Five targets were located along 2 lines; one target was located 10 cm directly in front of the home position and was represented by a *yellow circle* 1 cm in diameter. Four additional targets were located 5 and 7.5 cm to the left and right of the center target, 8.66 cm in front of the home position. The visuomotor distortion was introduced gradually until the cursor was translated 4 cm rightward with respect to the hand. This shift ensured that the *green cursor* (representing the hand) appeared to come from a central position. **c** Top view of experimental surface visible to subjects in the proprioceptive estimates tasks. One reference marker was located 10 cm directly in front of the home position and was represented visually by a *yellow disk*, 1 cm in diameter or proprioceptively (body midline). Two additional reference markers were located 5 cm to the left and right of the center reference marker, 8.66 cm in front of the home position. **d** Staircase and uncertainty range for the data of one subject for one reference marker. For the left panel, the staircase depicted with triangles illustrated the adjusted hand position across trials for the staircase starting at 3 cm leftward of the reference marker, while the squares illustrate the staircase starting 3 cm rightward. In the right panel, *circles* represent the mean percentage of responses by which the subject reported the hand was left of the visual reference marker across various hand locations. The *green line* intersecting the *x*-axis shows the bias (the point at which the probability of responding left was 50 %), while the *blue lines* depict the uncertainty range (the difference between the values at which the probability of responding left was 25 and 75 %)

was generated perpendicular to the grooved wall (Henriques and Soechting 2003). In this task, there were 60 trials, 12 trials for each target.

No-cursor reaching task: reach errors assessment

Immediately after the aligned reach training task, subjects reached to the same five targets 3 times each without a cursor (Box 2 in Fig. 2). 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 five reach targets would appear. Subjects were asked to reach to the visible target (as in the previous task) with the robot handle without the cursor or any visual feedback of their hand. Once the reach movement was complete (final position was held for 250 ms), the target and the home position disappeared. This cued subjects to actively move their unseen hand back to the home position along a constrained path to begin the next trial. This task was completed twice by each hand, first by the untrained hand from the previous training task (Boxes 2 and 4 in Fig. 2) and then by the trained hand (Boxes 6 and 8 in Fig. 2).

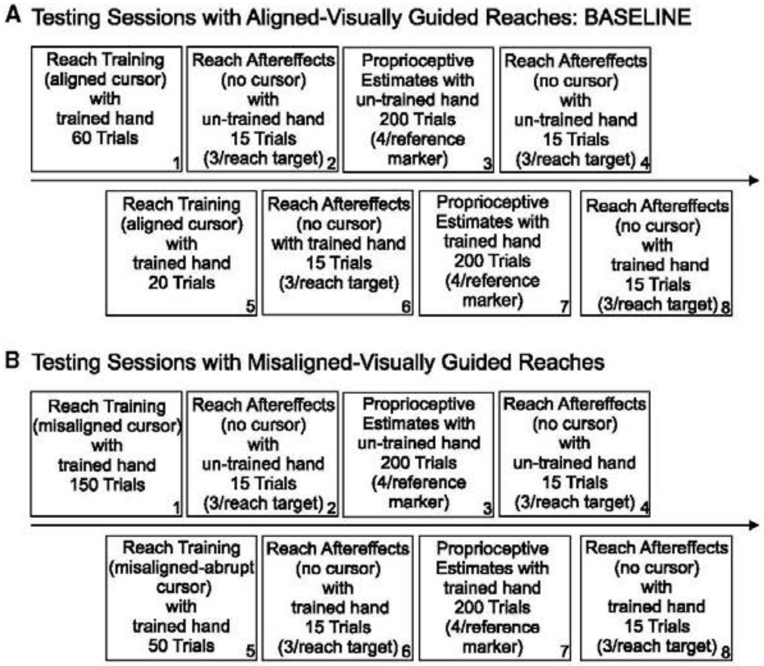

Fig. 2 Breakdown of the testing sessions within each experiment. **a** Testing session(s) which provided baseline measures of performance. Subjects began their first testing session by reaching to visual targets with their right or left hand (trained hand) while a cursor accurately represented the location of their unseen hand (*box* 1). After completing 60 visually guided reach trials, subjects then reached with their opposite hand (untrained hand) to each of the 5 reach targets, three trials each, without a cursor to assess visuomotor adaptation (reach aftereffect trials, *box* 2). Subjects then completed 200 proprioceptive estimates trials with their untrained hand (*box* 3). After completing the proprioceptive estimate task, subjects completed 15 reaches without the cursor, 3 reaches to all 5 target positions with their untrained hand (*box* 4). Then, they completed a short aligned training task with the trained hand (*box* 5). After completing 20 visually guided reach trials, subjects (trained hand) completed 15 reach trials without the cursor using the trained hand (*box* 6). Subjects then completed 200 proprioceptive estimates trials with their trained hand (*box* 7). The end of this session consisted of 15 reach trials, without a cursor, using their trained hand (*box* 8). **b** In the testing session(s) completed on the second day of the experiment, subjects performed 150 visually guided reaching trials using their right or left trained hand in which the 4-cm rightwards distortion was introduced gradually (*box* 1). Subjects then performed the same tasks as on the first day with their untrained hand (*boxes* 2, 3 and 4). After completing these tasks, subjects completed 50 visually guided reaching trials with the trained hand with a misaligned cursor, which was presented abruptly (*box* 5). Then, subjects did the same tasks as done on the first day with their trained hand (*boxes* 6, 7 and 8)

Proprioceptive estimates task: sense of felt hand position assessment

In the proprioceptive estimate trials (Boxes 3 and 7 in Fig. 2), we determined the position at which subjects perceived their unseen hand was aligned with the four reference markers. A proprioceptive estimate trial began with subjects grasping the robot manipulandum that was positioned at the home position. Subjects were then to actively push the robot handle outwards along a constrained path to a location somewhere along the dotted line shown in Fig. 1b (dotted line is for illustration purposes only and was not visible to the subjects). Once the hand arrived at its final position, one of the three visual reference markers 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 four reference markers for the proprioceptive estimates were located along two lines, 8.66 or 10 cm, in front of the home position (yellow circles, Fig. 1c). One reference marker was located 10 cm directly in front of the home position and was represented visually (yellow disk, 1 cm in diameter) or proprioceptively. This proprioceptive reference marker position was based on an internal representation of body midline. Two additional visual reference markers were located 5 cm to the left and right of the center target, 8.66 cm in front of the home position. There were 200 trials in this task, 50 trials for each target.

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 (illustrated as triangles and squares in the left panel of Fig. 1d), that were adjusted independently and randomly interleaved. Each staircase began such that the hand was 3 cm to the left or right of the reference marker. The position of the hand was then adjusted over trials depending on subjects' 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 (Fig. 1d).

Misaligned reach training task

The tasks for the second testing session were similar to the first except for the reaching training tasks, which involved a misaligned cursor (Boxes 1 and 5 in Fig. 2b). In this misaligned reach training task, the cursor was translated 4 cm rightwards with respect to the actual hand location in the reach training task. To ensure that subjects were unaware of the visuomotor distortion, this shift in cursor position was introduced gradually over the first 41 reach training trials, and thus continue at this maximum cursor translation for the remaining 109 trials for this task (Box 1 in Fig. 2b) and for the subsequent task (Box 5 in Fig. 2b). This was done by shifting the start position of the hand 1.0 mm leftward every trial until it reached 4 cm. The same targets and cursor were used as those in the aligned reach training tasks. For the gradual translation task, there were 150 trials, 30 trials for each target. And for the abrupt translation task, there were 50 trials, 10 trials for each target. These tasks were completed by the trained hand in either the left- or right-hand training group.

Data analysis

Visuomotor adaptation

Directional deviations of the hand made during reaching trials without visual feedback were analyzed to assess motor adaptation. Since the cursor was shifted horizontally (to the right of actual hand position), we were only interested in errors in this horizontal direction. Reaching endpoint errors were defined as the horizontal difference between a movement vector (from the home position to reach endpoint) and reference vector (from the home position to the target). Reach errors at peak velocity were defined as the horizontal difference between a movement vector joining the home position and the position of the hand at peak velocity and the reference vector. Both of these errors, which we will refer as aftereffects (i.e., baseline values subtracted from adaptation results), were analyzed to determine whether subjects adapted their reaches to the targets after aiming with a translated cursor, and whether there were any changes in reach adaptation following the proprioceptive estimate trials. To compare the transfer of aftereffects following training with translated-cursor feedback from the trained to the untrained hand 2 Group (right hand trained vs. left hand trained) × 2 Training condition (aligned vs. translated cursor) × 2 Hand used (trained vs. untrained) × 2 Time (following reach training trials vs. following proprioceptive estimate trials), mixed ANOVAs were performed on reaching endpoints and reach errors at peak velocity. To assess intermanual transfer, we specifically looked at the difference between these no-cursor reaches following training with the aligned versus translated cursor in the untrained hand and also compared this to the differences for the trained hand. Hand used, Training condition and Time were treated as within-group variables, while Group was treated as a between-group variable. Additionally, due to our study goals, pairwise comparisons were made across three main factors (Group, Training, Hand used).

Finally, we assessed the extent of intermanual transfer using an independent t test to compare the aftereffects (to reduce factors in the analysis, we subtracted no-cursor reach errors on day 1 (baseline) from those on day 2, so that our new dependent variable was a difference in errors) of the trained and untrained hand for each hand; i.e., trained left hand (from the Left hand group) versus untrained left hand (from the Right hand group), and trained right hand (from the Right hand group) versus untrained right hand (from the Left hand group).

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, as illustrated in the right panel in Fig. 1d. From this logistic function, we calculated the bias (the point at which the probability of responding left was 50 %, shown in green) and uncertainty (the difference between the values at which the probability of responding left was 25 and 75 %, shown as blue lines). The bias value is a measure of subjects' accuracy of

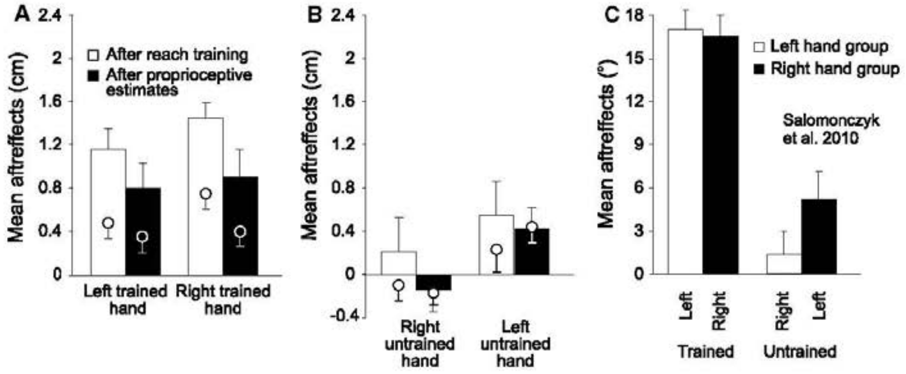

Fig. 3 Mean endpoint aftereffects (*bars*) and errors at peak velocity (*circles*) following reach training with misaligned visual feedback of the hand. **a** Values reflect baseline-subtracted aftereffect errors in the trained left and right hands (*left* and *right bars*, respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **b** Values reflect baseline-subtracted aftereffect errors in the untrained right and left hands (*left* and *right bars*, respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **c** Mean endpoint aftereffects from (Salomonczyk et al. 2010) for (*left* and *right*) trained hands and (*right* and *left*) untrained hands (*left* and *right bars*, respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). *Error bars* reflect standard error of the mean

proprioceptive sense of hand position, while the magnitude of the uncertainty range defines its precision (Cressman and Henriques 2009; Cressman et al. 2010).

Proprioceptive recalibration was assessed by comparing the proprioceptive biases or estimates of hand position after training with a translated cursor with those following an aligned cursor (baseline), not only for the trained hand, but also for the untrained hand, so that we could test for intermanual sensory transfer. To do this, we ran a 2 Group (right hand training vs. left hand training) × 2 Hand used (trained vs. untrained) × 2 Training condition (aligned vs. translated cursor) × 4 Marker location (5 cm to the right vs. 5 cm to the left vs. middle visual vs. middle proprioceptive) mixed ANOVA on the proprioceptive estimates or biases. A similar mixed ANOVA was also run to compare the uncertainty values. Again, due to our interest in examining whether the intermanual transfer differs across hands, we followed these ANOVAs with preplanned comparisons.

All ANOVA results are reported with Greenhouse–Geisser corrected P values. Differences with a probability of 0.05 were considered to be significant. A Bonferroni correction was applied to all preplanned pairwise comparisons.

Results

Visuomotor adaptation

Figure 3 depicts mean reaching endpoint errors (aftereffects) for (A) the left and right trained hands, and (B) the right and left untrained hands immediately following reach training trials (white bars) and following the proprioceptive estimate trials (black bars) relative to baseline performance (i.e., errors achieved on the first day of testing after training with an aligned cursor were subtracted from errors achieved after reaching with a translated cursor). No-cursor reaches were significantly shifted in the direction of the distortion following translated-cursor training compared to aligned-cursor training ($F(1, 33) = 45.60$, $p < .001$). But as expected, the changes in open-loop reaches varied depending on whether they were completed by the trained or untrained hand ($F(1, 33) = 21.82$, $p < .001$). However, given the low power of higher-order interactions, we were not able to find a significant three-way interaction when including the factor of Group ($F(1, 33) < 1$, $p = .532$), nor a four-way interaction when including Group and Time ($F(1, 33) < 1$, $p = .276$). Thus, we proceeded to our planned, pairwise comparisons for the trained hand and the untrained hand, in order to explore the difference in performance between aligned and translated training conditions, as a function of Group. In the next two paragraphs, we first report pairwise comparisons for the trained hand and then untrained hand for each group.

For the trained hands, the significant shift in no-cursor reaches for both the left and right hands was on average 1 cm ($F(1, 33) = 33.681$, $p < .001$) and 1.2 cm ($F(1, 33) = 53.090$, $p < .001$), respectively. The fact that there was no further interaction across Groups ($F(1, 33) < 1$) suggests that this adaptation was achieved, and by a similar amount, for both the left and right trained hands. Analysis also revealed smaller reach aftereffects following the proprioceptive estimate trials compared to those immediately after the reach training trials ($F(1, 33) = 4.512$, $p = .041$). Specifically, reach aftereffects of 1.18 and 1.45 cm were observed in the first set of no-cursor reach trials (white bars in Fig. 3a) for the left and right hands, respectively, while the following set of no-cursor reaches (black bars in Fig. 3a) revealed that reach aftereffects had diminished to 0.8 and 0.9 cm for the left and right hands, respectively. Despite the decay in reach aftereffects following the proprioceptive estimate trials compared to those immediately after reach training, the aftereffects for the trained hands were still significantly different from baseline conditions.

On the other hand, reaching errors in the untrained hand showed evidence of intermanual transfer only in the untrained left hand following opposite right-hand adaptation ($F(1, 33) = 5.412$, $p = .026$), both when measured right before the proprioceptive estimate task and again right after, despite a small but non-significant decay in aftereffects over time ($F(1, 33) = 1.298$, $p = .263$). Changes in reach endpoint for the untrained right hand did not differ following opposite left-hand training ($F(1, 33) < 1$, $p = .856$). In other words, the untrained right hand (dominant hand) did not benefit from the left-hand (non-dominant) training, while the left hand benefited from the dominant hand (opposite hand) training. Analysis of reach errors at peak velocity (as indicated by the circles in Fig. 3a, b) revealed a similar pattern of results. Specifically, reach deviations at peak velocity in the untrained hand showed evidence of intermanual transfer only in the untrained left-hand following opposite right-hand adaptation ($F(1, 33) = 4.896$, $p = .034$), while reach errors at peak velocity for the untrained right hand did not differ following opposite left-hand training ($F(1, 33) < 1$, $p = .543$). This suggests that endpoint accuracy and initial directional errors transferred between hands, but from right to left not from left to right.

In order to assess the extent of the intermanual transfer to the left untrained hand, we compared the aftereffects (for trials following both reach training and proprioceptive estimates) of this untrained hand with those of the trained left hand from the other group. We found endpoint reach errors in the untrained left hand were less than aftereffects of the trained left hand, but not significantly ($t(33) = 1.85$, $p = .073$), while difference between the trained and untrained right hand was significant ($t(33) = 4.38$, $p < .001$). These findings confirm that the untrained left hand (non-dominant) benefited from previous training with the right hand (dominant) using a gradually introduced translated cursor; however, the untrained right hand did not benefit from the prior training with the left hand.

Interestingly, Salomonczyk et al. (2010) found similar results in their study of intermanual motor transfer when they introduced a 30° rotation to two subjects groups, one group which trained with the right hand and the other which trained with the left hand (Fig. 3c). Specifically, after reaching with a rotated cursor subjects adapted their reaches in both the right and left trained hands ($F(1, 44) = 265.4$, $p < .001$), however, only following right-hand adaptation did the opposite untrained left hand show a significant difference in endpoint errors (5°; $F(1, 44) = 7.646$, $p = .008$). In other words, the right untrained hand did not differ following opposite left-hand training (<1°; $F(1, 44) < 1$, $p = .935$). Also, analysis of reach errors at peak velocity revealed the same pattern of effects. These results suggest that prior training with the right hand led to a transfer of learning to the unexposed left hand.

Proprioceptive recalibration

Bias

Figure 4 depicts a two-dimensional view of the positions at which subjects in the left (A)- and right (B)-hand training groups perceived their hands to be aligned with the reference markers after training with an aligned (empty symbols) and translated cursor (filled symbols) for the trained hand (squares) and untrained hand (triangles). While we found a significant change in proprioceptive biases after adapting to a translated cursor ($F(1, 33) = 8.449$, $p = .006$), we found no significant three-way interaction including Hand used and Group ($F(1, 33) < 1$, $p = .529$) or four-way interaction and including Hand used, Group and Reference marker ($F(3, 99) = 1.062$, $p > .05$). We then continued to our planned comparisons for the trained hand and the untrained hand in order to investigate the performance difference between aligned and translated training conditions, as a function of Group.

Following training with aligned-cursor feedback, subjects estimated their trained hand was aligned with the reference marker when it was on average 1.17 cm to the right of it (left-hand training group) or .46 cm to the left of it (right-hand training group). After subjects trained with the translated cursor, the bias of their trained hand (squares) estimates of hand position shifted to the left, on average 0.65 cm, and thus in the direction of the visuomotor distortion ($F(1, 33) = 12.350$, $p < .001$). The magnitude of this change is shown in the left bars in Fig. 4c. This shift in proprioceptive estimates was comparable across the left- and right-hand training groups ($F(1, 33) < 1$, $p = .721$) and again comparable across the four reference markers ($F(3, 99) = 2.019$, $p = .150$), regardless of whether the center reference marker was proprioceptive or visual for the left ($p = 1$)- and right-hand ($p = .350$) training groups.

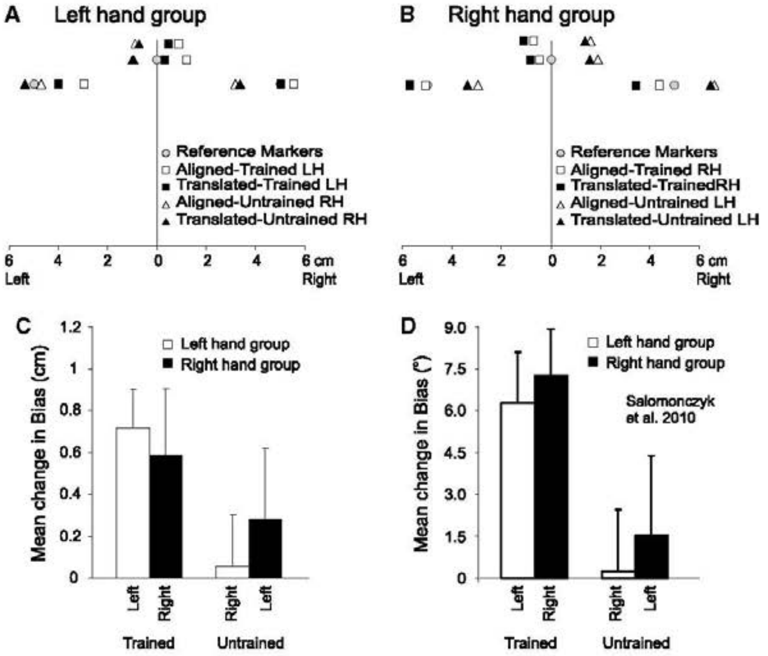

Fig. 4 Proprioceptive estimates for the trained and untrained hands. **a** Left-hand training group mean 2D biases in the proprioceptive estimate tasks for the left trained (*squares*) and right untrained (*triangles*) hands following left-hand training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. The actual reference marker positions are represented as *filled gray circles*. **b** Right-hand training group mean 2D biases in the proprioceptive estimate tasks for the right trained (*squares*) and left untrained (*triangles*) hands following training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. Proprioceptive estimates relative to the body midline have been shifted above those made at visual markers for both **a** and **b** (*above*) to avoid overlap. **c** Mean change in bias for the (*left* and *right*) trained hands and (*right* and *left*) untrained hands (*left* and *right bars*, respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). **d** Mean change in bias from (Salomonczyk et al. 2010). *Error bars* reflect standard error of the mean

While the positions at which subjects felt their left and right trained hands (squares in Fig. 4a, b) to be at a reference marker were significantly shifted following training with translated feedback, when we measured the untrained right and left hands, the mean biases were shifted only .05 and .27 cm leftwards (triangles in Fig. 4a, b and bars on the right in Fig. 4c), respectively. These shifts were not statistically significant from biases following training with the aligned-cursor feedback (right hand: $F(1, 33) < 1$, $p = .848$; left hand: $F(1, 33) < 1$, $p = .349$).

Again, our findings are consistent with previous results observed by Salomonczyk et al. (2010) (Fig. 4d). Specifically, they found that the position at which subjects' felt their trained hand coincided with the reference marker was shifted leftwards by 6.6° (approximately 20 % of the distortion introduced) after training with a 30° rotated cursor compared to after reaching with an aligned cursor ($F(1, 44) = 28.8$, $p < .001$). While the mean biases in the untrained left and right hands were shifted by 1.50° and .14° leftwards, respectively, however, these shifts were not statistically significant ($F(1, 44) < 1$, $p = .953$; $F(1, 44) < 1$, $p = .564$, respectively).

Uncertainty

Figure 5 depicts the magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (white bars) and translated (white dashed bars) cursor feedback, and the right and left untrained hands following reach training with aligned (black bars) and translated (black dashed bars) cursor feedback. The uncertainty ranges did not differ across any of the factors; nor were there any interactions ($p > 0.05$).

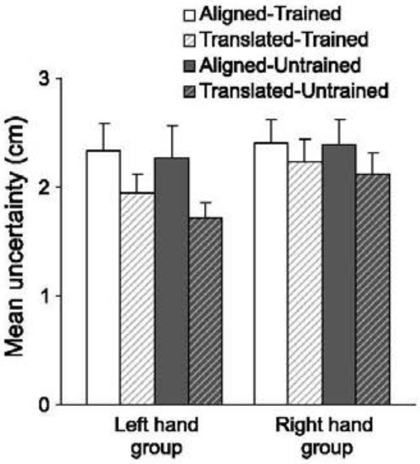

Fig. 5 Magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (*white bars*) and translated (*white dashed bars*) hand-cursor feedback. Magnitude of uncertainty ranges for the right and left untrained hands is also displayed following reach training with aligned (*black bars*) and translated (*black dashed bars*) cursor feedback. *Error bars* reflect standard error of the mean

Discussion

We sought to assess the extent that adapting to a translated cursor leads to transfer of motor adaptation to the opposite hand, and whether this transfer differs between the dominant and non-dominant hands. Additionally, we wanted to determine whether changes in hand proprioception that occur with the trained hand following motor adaptation transfer to the untrained hand. We found intermanual motor transfer to the left untrained hand after subjects trained their right hand to reach with translated visual feedback of their hand, while transfer from the left trained hand to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike motor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

Motor transfer and arm asymmetry

While visuomotor adaptation was observed to the same extent in both the left and right trained hands of right-handed individuals following adaptation to a visuomotor distortion, these findings were not symmetrically transferred to the untrained hands. Small but significant reach aftereffects were observed in the untrained left hand following training with the right hand, suggesting some of the motor adaptation of the right hand had been transferred to the untrained left hand. Unsurprisingly, these transferred aftereffects were smaller than those observed in the trained left hand, suggesting that transfer between the two hands is incomplete. No transfer of reach aftereffects was observed in the untrained right hand following training with the left hand.

Our results are consistent with previous findings from our laboratory (Salomonczyk et al. 2010), in which a different distortion was employed. Salomonczyk et al. found that subjects adapted their reaches in both the right and left trained hands (and with comparable magnitude) after training with a 30° CW rotated cursor; however, intermanual transfer only occurred after right-hand adaptation and only the untrained left hand produced significant aftereffects. Together, these results suggest the asymmetry in transfer is not due to the type of distortion (i.e., translated or rotated cursor), as it occurred in both cases. While adaptation to a translated cursor may result in greater generalization overall (Ghahramani et al. 1996; Vetter et al. 1999; Cressman and Henriques 2009), it did not result in greater or different patterns of intermanual transfer compared to that produced following adaptation to a comparably sized visuomotor rotation (Salomonczyk et al. 2010). Specifically, from the aftereffects observed in the present study and those by Salomonczyk et al.'s (2010) (Fig. 3c), it appears that there were no real differences in the size and pattern of the intermanual motor regardless of the extent of motor adaptation achieved.

Our pattern of intermanual motor transfer, based on measuring changes in endpoint errors in the open-loop reaches (i.e., aftereffects), is different from that found by Sainburg and Wang (2002) and Wang et al. (2011) when assessing how well the untrained hand could adapt to the same perturbation experience by the trained hand. The authors found that adaptation of both the untrained left and untrained right hand was facilitated with prior training with the opposite hand to the same visuomotor rotation. However, the measures by which these two untrained arms showed this advantage, or transfer, differed depending on the arm. Specifically, final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. The asymmetries in their studies differ from our own in that we found evidence of transfer of initial directional accuracy and final position accuracy to the non-dominant hand, while we also failed to observe either effect from the non-dominant to the dominant hand. The difference between our studies (including that by Salomonczyk et al. (2010)) and theirs may have to do with how we assessed adaptation and transfer. In Sainburg and Wang's (2002) paradigm, as well as other studies on intermanual transfer, the untrained hand was exposed to the distortion and the learning rate (across trials) was assessed. Intermanual transfer is indicated by a steeper learning rate (also known as savings) as well as a smaller deviation in the first trials with the untrained hand following opposite-hand training. However, we assessed intermanual transfer by examining directional errors at peak velocity and endpoint errors during open-loop reaches to determine the magnitude of transfer. One explanation for this inconsistency, as outlined above, could be that direction and pattern of asymmetry of intermanual transfer differs depending on the measures of assessment. However, research from our laboratory using a different paradigm (Balitsky Thompson and Henriques 2010) where intermanual transfer was assessed by measuring facilitation following opposite-hand training revealed facilitation only from the right (dominant) arm to the left (non-dominant) arm. This pattern of transfer occurred across different magnitudes of distortion (45°, 60°, 75°) and different feedback representations (cursor vs. video image of the hand). Thus, this motor transfer to only the non-dominant arm found in three of ours studies (separate subjects and even different equipment for the Balitsky Thompson and Henriques study) may be beyond merely how transfer was measured, or the extent of motor adaptation. Another possible explanation of these different results in our study and studies of Sainburg and Wang is that the magnitude of aftereffects in our study was around 30 % of the visuomotor distortion, so that learning may not have been complete, and thus may have influenced the direction and the extent of the intermanual transfer.

Our observed asymmetric transfer is similar to transfer found by Redding and Wallace (2008) following adaptation to displacing prisms. The authors found that aftereffects (as assessed by reaches made following removal of the prisms) transferred from the right trained hand to the left untrained hand but not vice versa. The magnitude of transfer, as in our study, was approximately one-third of the aftereffects observed in the trained hand. These authors suggest that this asymmetric transfer between the right and left trained hands is due to symmetrically lateralized limb control but asymmetrical spatial mapping, where the right limb is represented in both hemispheres, while the left limb is represented only in the right hemisphere (Corbetta et al. 1993; Farne et al. 2003; Butler et al. 2004). The asymmetrical motor transfer of reach aftereffects we observe in the current study is consistent with this proposal.

Proprioceptive transfer and arm symmetry

We used a sensory estimation task that did not require any goal-directed movements, to assess proprioceptive recalibration independent of motor changes. Our findings replicate those from previous studies (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Salomonczyk et al. 2012) in that subjects experienced a shift in the position at which they felt their hand was aligned with a reference marker by roughly 20 % of the visuomotor distortion. However, proprioceptive recalibration did not transfer from the dominant or non-dominant trained to the opposite untrained hand. In particular, the mean biases of the untrained right and left hands were shifted only .05 and .27 cm leftwards, respectively, following reach training with a translated cursor compared to reach training with an aligned cursor, and these shifts were not statistically significant. Training with rotated visual hand feedback revealed a similar lack of transfer between the hands. Specifically, when Salomonczyk et al. (2010) introduced a 30° rotation to left- and right-hand trained groups, the authors found that subjects recalibrated proprioception equivalently in both groups, while the mean biases remained unchanged following opposite-hand training. Of course, given that proprioceptive change is much smaller than the change in reach movements (aftereffects) following visuomotor adaptation, it is possible that the felt position of untrained hand is shifted but by an amount that it is too small to detect. The magnitude of proprioceptive recalibration is typically a third of the aftereffects (Cressman and Henriques 2009, 2010), and in this study, the relative change in felt position for the trained hand (compared to the aftereffects) was closer to 70 %. Thus, given that aftereffects produced with the untrained left hand were about 0.6 cm in size, then the 33 % change in the proprioceptive perception of this hand would be about 0.2 cm, while a 70 % change would be closer to 0.4 cm. Indeed, we do find that the change in bias of the left hand was closer to 0.4 cm (see right black bar in Fig. 4c). However, given that this shift was not large enough to be detected statistically, we must conclude that hand proprioception was not changed for the untrained hands.

We assume that changes in biases of the trained hand following reach training are due to changes in proprioceptive estimates of the trained hand and not to some changes in the representation of visual space. This is based on the fact that in the current study, as well as in previous results, we have shown change in perceived hand position is equivalent between visual and proprioceptive (the body midline) markers (Cressman and Henriques 2009; Salomonczyk et al. 2011). The present results further argue against a possible shift in the visual representation of space following adaptation, as changes in bias for the trained and untrained hands would be similar if the visual representation of the marker was shifted. Indeed, this was not observed.

Several studies have suggested that the two arms may be specialized at using different types of sensory information for localizing a target. For instance, Goble and Brown (2008) have suggested that the left limb is better at matching proprioceptive targets and the right limb for matching visual targets. However, we did not find similar asymmetries between the two hands in our sensory task. Moreover, Carson et al. (1990) and Jones et al. (2010, 2012) found that right-handed participants estimated their hand location with error magnitudes between the two hands, although errors were opposite in direction. Additionally, Jones et al. (2010, 2012) reported that the magnitude of proprioceptive biases and uncertainty ranges across the two hands, measured without a preceding reach training task, did not differ at all. In the present study, we found the same magnitude of proprioceptive biases when subjects judged the right hand with respect to a body midline (i.e., proprioceptive) and visual reference markers.

In summary, we found no arm-dependent differences in either proprioceptive estimates or unseen hand movements made to visual targets. Moreover, given that we did not find evidence of proprioceptive recalibration transferring between hands, it appears that unlike visuomotor adaptation, proprioceptive recalibration is specific to the hand exposed to the distortion. Further studies are required to characterize motor adaptation and sensory recalibration and determine the extent that these two processes are responsible for intermanual transfer of motor adaptation.

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RESEARCH ARTICLE

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., ~22.5°; 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 uniformed 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

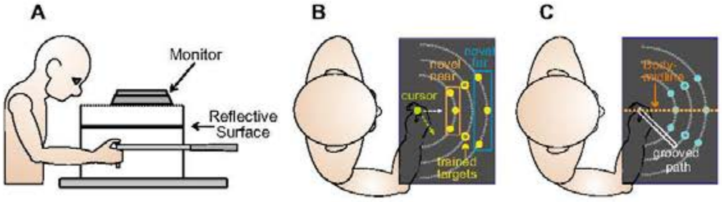

Fig. 1 Experimental setup and design. **a** Side view of the experimental setup. **b, c** Top view of experimental surface visible to subjects. The home position was located approximately 20 cm directly in front of subjects' midline and is represented by a hand cursor (1-cm-diameter *green disk*) in (**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)

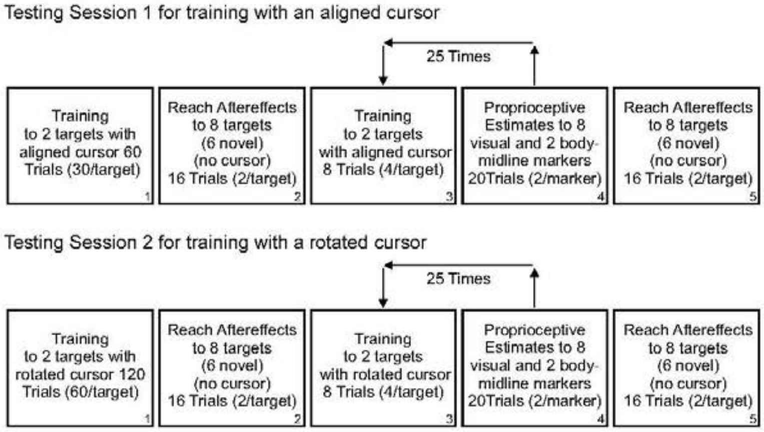

Fig. 2 Schematic showing the order in which the tasks were completed within a testing session. Both testing sessions followed the same order of tasks. The difference between the sessions was the visual feedback provided in the reach training tasks. The cursor was either aligned with the hand (*session 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 30º 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) × 2 Epoch (trials completed before vs. after the proprioceptive estimate task) × 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°), Fig. 3, middle gray bar] and for the novel targets [(15.1° and 11° 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 generalization across novel target locations, in that change in angle at peak velocity did not differ between trained and novel targets ($F(2,24) = .325$; $p = .622$).

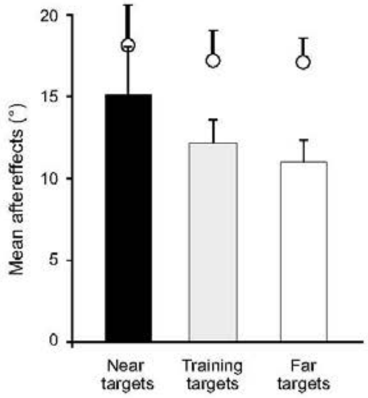

Fig. 3 Reach aftereffects: difference in mean angular reach endpoint error for the no-cursor reaches after training with misaligned visual feedback for training targets, novel-near targets, and novel-far targets relative to baseline performance. *Circles* represent mean changes in reaching errors at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

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° 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°, while the change was 9.4° and 6.3° 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

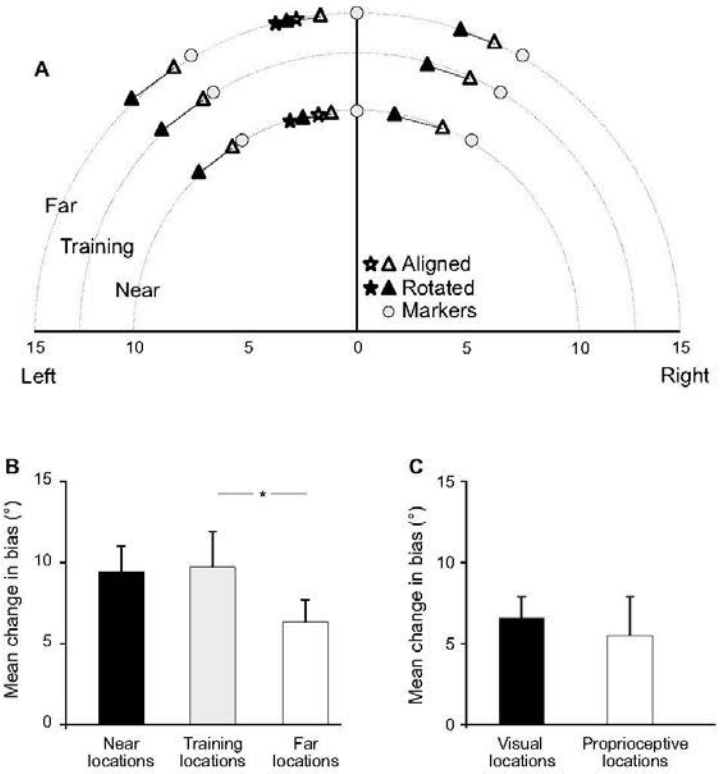

Fig. 4 Proprioceptive biases following training with aligned and rotated visual feedback of the hand. **a** Mean 2D biases in the proprioceptive estimate tasks relative to the reference marker locations (*gray disks*) after training with aligned visual feedback (*unfilled symbols*) and after training 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 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

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 ($F(1,12) = .211$; $p = .654$). 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 Rugy 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 farthest 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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