REACH ADAPTATION AND PROPRIOCEPTIVE RECALIBRATION FOLLOWING TERMINAL VISUAL FEEDBACK OF THE HAND

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ABSTRACT

Reaches are adapted and proprioceptive sense of hand position is partially recalibrated after training with continuous, misaligned visual feedback. When visual feedback is provided only at the end of the movement, it is unclear if similar changes arise. To test this, participants reached to targets, first with aligned-cursor, then three times with rotated-cursor. After each block, we measured no-cursor reaches and perceived felt hand positions relative to a reference marker. We found that reach aftereffects were slightly smaller than that following training with continuous visual feedback. Additionally, terminal feedback participants incrementally recalibrated their sense of felt hand position over the rotated training blocks. Final proprioceptive recalibration levels were comparable to those in our continuous feedback study. Thus, compared to continuous feedback findings, terminal feedback produced significant, yet smaller, reach aftereffects but similar changes in hand proprioception. Taken together, terminal feedback is sufficient to drive motor adaptation and proprioceptive recalibration.

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Introduction

When reaching to an object, visual and proprioceptive information may be used to help localize the hand in space and provide information regarding reach accuracy. If one repeatedly misses the target, because visual feedback regarding the hand position has been misaligned from the actual hand position, reaches are gradually adjusted to once again produce accurate movements. This process is referred to as visuomotor adaptation and is a type of motor learning where our central nervous system updates motor plans to correct for movement errors (Krakauer, 2009; Krakauer, Ghilardi, & Ghez, 1999; Krakauer, Pine, Ghilardi, & Ghez, 2000; Mazzoni & Krakauer, 2006; Redding & Wallace, 2000; Simani, McGuire, & Sabes, 2007). Visuomotor adaption is measured through aftereffects, which are reach errors that persist after the visual distortion has been removed by either eliminating the hand-cursor or reintroducing an aligned hand-cursor.

Review of Literature

Goal-Directed Movement

We take for granted the complex network and computations required for the simplest movement. We reach for a cup of coffee with ease, and even if our reach is slightly off target during its initial movement, we correct our errors seemingly effortlessly. A goal-directed movement, like reaching for a cup of coffee, is a voluntary, purposeful action that is under control of the central nervous system and the cerebral cortex (Wise & Shadmehr, 2002). For goal-directed movement, a motor plan is needed, and visual and proprioceptive information about the hand and object must be integrated (Jeannerod, 1988). Because we live in a variable environment, we need to obtain new skills and adapt pre-existing skills to suit our changing environment and bodies. Further, goal-directed movements improve with practice and learning. In examining goal-directed movements, I will review relevant brain areas involved, and briefly describe some theoretical concepts pertaining to goal-directed movement, including what a motor program is, and basic mechanisms that govern movement.

Reach-related brain areas

There are several brain areas required to coordinate goal-directed movement. In the primate cerebral cortex, the following areas are important for movement planning and execution: posterior parietal cortex (PPC); frontal lobe regions including premotor areas (ventral premotor area (PMv) and dorsal premotor area (PMd)), the primary motor area (M1), supplementary motor area (SMA), and cingulate motor area (CMA); and the cerebellum.

Before initiating a reach to a coffee cup, the brain must code the cup's and our hand's locations in three-dimensional space based on two-dimensional visual coordinates, and/or on proprioceptive information. Localization of objects, including the reaching hand, involves areas in the parieto-occipital region of the

PPC (Culham & Valyear, 2006; Fogassi & Luppino, 2005). Patients with PPC damage, like optic ataxia patients, have shown deficits in visually exploring space, programming and arranging skilled movements, and reaching to visual targets (Culham & Kanwisher, 2001). Recent fMRI findings have corroborated earlier conclusions from studies on patients with optic ataxia, revealing that several areas in the PPC are implicated in visually-guided reaching (Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006). Several primate electrophysiology and human neuroimaging studies show that various areas in PPC (Fig. 1), such as MIP, area V6a, area 5, are important in coding the location of reach targets, with some researchers classifying MIP and V6a as part of a parietal reach region (PRR) (Andersen & Buneo, 2002; Buneo, Jarvis, Batista, & Andersen, 2002; Culham et al., 2006; Culham & Valyear, 2006). Some fMRI studies suggest that the human region, medial occipito-parietal junction (mOPJ) may be a homologue to the PRR, and other neuroimaging studies have proposed that the human medial intraparietal sulcus (mIPS) may be functionally equivalent to MIP (Culham & Kanwisher, 2001; Culham & Valyear, 2006). Thus, in terms of reaching, PPC may be critical for spatial coding of targets and effectors for goal-directed movement. Much of this information from the PPC is the sent to the frontal lobe (Caminiti, Ferraina, & Battaglia Mayer, 1998).

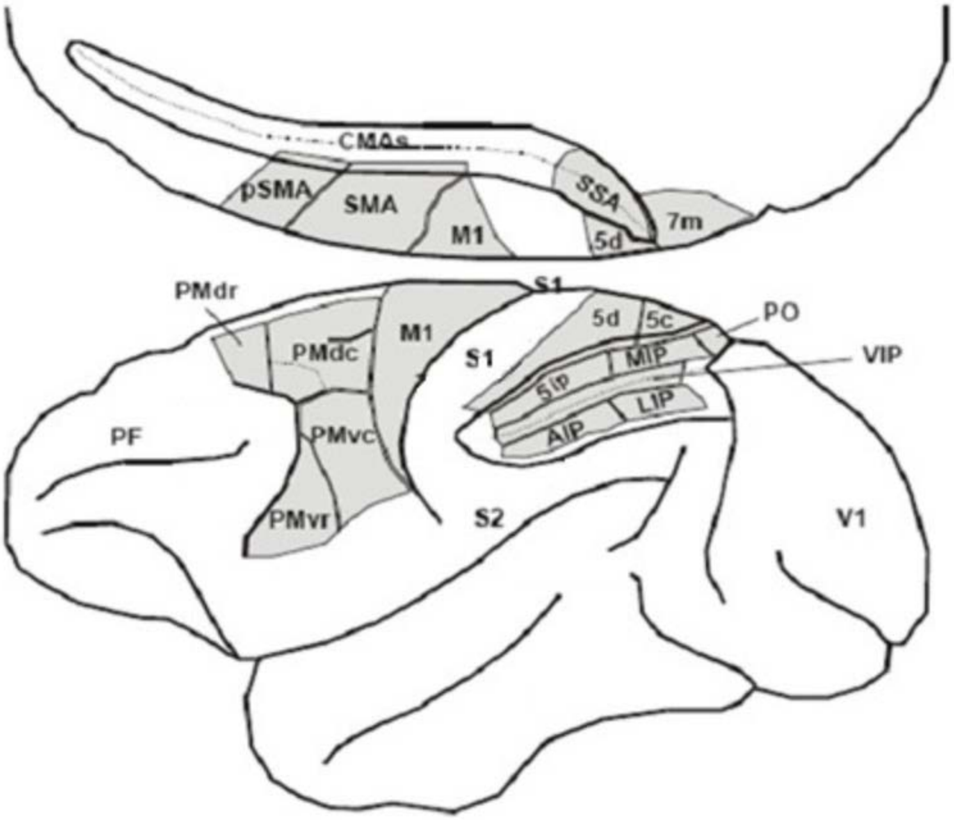

Figure 1: Brain areas relevant to goal-directed movement. In the Posterior Parietal Cortex (PPC): medial intraparietal cortex (MIP), anterior intraparietal cortex (AIP), lateral intraparietal cortex (LIP), ventral intrapateital cortex (VIP), area 5, and parieto-occipital area (PO); dorsal premotor cortex (Pmd), ventral premotor cortex (Pmv), primary motor cortex (M1), supplementary motor area (SMA), cingulate motor area (CMA). Not featured here is the cerebellum. (Adapted from Shadmehr and Wise, 2005)

In the frontal lobe, premotor areas PMv and PMd receive spatial and multisensory information from the parietal cortex to further develop motor plans. These areas are specifically and preferentially active for coding targets of an upcoming movement of the arm (Schwartz, Moran, & Reina, 2004; Shadmehr & Krakauer, 2008). These premotor areas, as well as the primary motor cortex, receive indirect inputs from the basal ganglia and cerebellum via the ventrolateral thalamic nucleus (Kalaska, 2009). Premotor neurons project to M1 as well as directly to the spinal cord, along with M1 projections, to make up the corticospinal pathway (Kantak, Stinear, Buch, & Cohen, 2012). PM areas and M1 also send information to the spinal cord indirectly via the brainstem. Based on electrophysiology, patient, and neuroimaging studies, these premotor areas appear to be an important node for movement planning, specifically the kinematics involved in moving the arm and hand (Boussaoud & Wise, 1993; Caminiti et al., 1998; Hoshi & Tanji, 2007; Kantak et al., 2012).

Also in the frontal lobe is M1, rostral to the central sulcus. M1 receives direct input from the primary somatosensory cortex (S1), the PPC, the premotor areas, as well as the SMA, and CMA. Neurophysiological research has shown that M1 is critical in initiating and specifying movement direction, plus the torques (forces) for the required muscle activity: M1 cells do not appear to reflect any single movement parameter, but these cells are active for initiating and executing goal-directed movement (Dayan & Cohen, 2011; Kalaska, 2009; Scott, 2003). Initial position and orientation of the arm appears to modulate the neural activity related to preparing for and executing arm movements (Caminiti et al., 1998; Scott & Kalaska, 1997).

These same brain areas are involved in motor learning. Recent neuroimaging studies have shown when people learn novel button-pressing sequences, the initial learning phase (related to large, quick improvements) is associated with increased activation in premotor areas, and parietal regions, and decreased activation in M1. In contrast, the later learning phase, and the phase after the skill has been learned, is associated with increased activation in M1 (Dayan & Cohen, 2011).

No less important for motor control is the cerebellum. This neuron-dense structure located at the base of the cerebral cortex receives sensory input from the spinal cord, motor information from the cerebral cortex and vestibular information from the inner ear's vestibular organs. Patients with cerebellar damage show impaired motor performance, such as poor coordination (Martin, Keating, Goodkin, Bastian, & Thach, 1996b; Shadmehr & Krakauer, 2008; Timmann et al., 2010). Numerous patient studies and imaging studies have also demonstrated that the cerebellum plays an important role in motor learning and correcting motor errors (Akshoomoff, Courchesne, Press, & Iragui, 1992; Dirnberger, Novak, & Nasel, 2013 ; Imamizu et al., 2000; Küper et al., 2014; Miall, Christensen, Cain, & J., 2007; Narayana et al., 2014; Sanes, Dimitrov, & Hallett, 1990; Shmuelof, Yang, Caffo, Mazzoni, & Krakauer, 2014; Tzvi, Münte, & Krämer, 2014; Wadden, Brown, Maletsky, & Boyd, 2013; Weiner, Hallett, & Funkenstein, 1983). In brief, the cerebellum is integral for accurate, goal-directed reaches and motor learning.

Theoretical concepts

For goal-directed reaches, such as the arm and hand movements required for reaching to a coffee cup, a motor program is needed. Keele (1968) points out that a motor program is not the movement itself, but is “a set of muscle commands that are structured before a movement sequence begins, and that allows the entire sequence to be carried out” (p. 387). There are ostensibly endless possible ways to move from one posture to another: This is called the degrees of freedom problem. For a goal-directed reach, there are seven degrees of freedom based on the shoulder, elbow, and wrist joints and twenty more degrees of freedom based on the muscles. Fortunately, actions are organized and stored so that the degrees of freedom are reduced when a particular action is required (Jeannerod, 1988).

To reach to a target, the CNS must generate motor commands to produce the desired endpoint, the hand path to get there, and the necessary change in joint angles (inverse kinematics). Next, the CNS needs to compute the necessary muscle forces and torques to produce the joint motion (inverse dynamics). Besides inverse calculations, the CNS also generates forward kinematics and dynamics in order to recalculate and predict hand movement’s states both during and after the movement (Wise & Shadmehr, 2002).

The inverse model reflects the information and computations necessary to generate a motor command that will elicit the desired action based on the feedback, or sensory information that is available (Flanagan, Vetter, Johansson, & Wolpert, 2003; Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Kawato, 1998). The forward model predicts 1) the necessary motor commands to complete an action, and 2) the sensory consequences associated with said action. With the forward model, an action’s outcome can be estimated prior to receiving any sensory feedback by using motor outflow (i.e., an action’s efference copy), to overcome delays in sensory feedback. Errors between the desired and actual sensory outcome provide information to update these internal models

(Flanagan et al., 2003; Wise & Shadmehr, 2002; Wolpert et al., 1995). When the environment is changing, and both inverse computations and the forward model's predictions are initially inaccurate (Wise & Shadmehr, 2002; Wolpert, Miall, & Kawato, 1998), but with continued practice, these internal models are modified or updated accordingly. These inverse and forward calculations, or internal models, contribute to both well-learned movements, and learning new movements (Wise & Shadmehr, 2002).

Motor learning and adaptation

Motor learning involves modifying movements in response to a changing body as well as a changing environment. In other words, movements need to be modified as we grow, age or become injured (internal changes) or when interacting with objects and the environment (Wolpert, Ghahramani, & Flanagan, 2001), such as using tools or navigating a different medium, (e.g., walking on pavement versus walking on sand). Simply stated, motor learning includes acquiring new skills and modifying current ones, which are stored in procedural memory. Skill acquisition involves acquiring a novel behavior; an addition to the motor repertoire. Learning to pick up a small, plastic cup for the first time, or learning to row with sculls, are examples of skill acquisition: A child learns to coordinate her muscles and torques to accurately reach to, grasp and lift a cup, and the novice rower learns to coordinate hand motion and leg drive. Motor adaptation arises when a pre-existing skill is updated to suit the current environment (Krakauer, 2009): A child who wants a large, ceramic cup must adapt her previous skill, adjusting the joint angles and torques she previously used in order to pick up the heavier cup. Rowing with a different type of oar is another example of motor adaptation. Thus, adaptation requires compensating for changes in the original relationship between the actual movement and the expected motor outcome by modifying or forming a new internal model. As a result, ideally, performance of a well-learned skill under novel conditions returns to original baseline performance following adaptation (Wolpert et al., 1995).

A type of motor adaptation well studied in the lab is visuomotor adaptation, which occurs when a mismatch is introduced between our seen movements and our actual arm movements. One such way a mismatch is introduced is when visual feedback of the hand (and/or target) is altered; for example, by translating or rotating the effector's visible position (i.e., with a hand cursor or prism goggles) compared to actual position (Buch, Young, & Contreras-Vidal, 2003; Cohen, 1967; Cressman & Henriques, 2009; Cressman & Henriques, 2012; Hay & Pick, 1966; Henriques & Cressman, 2012; Klassen, Tong, & Flanagan, 2005; Krakauer, Ghez, & F., 2005; Krakauer et al., 1999; Mazzoni & Krakauer, 2006; Rabe et al., 2009; Redding & Wallace, 1988a, 2001; Salomonczyk, Cressman, & Henriques, 2011; Salomonczyk, Henriques, & Cressman, 2012; Tong & Flanagan, 2003). If the altered visual feedback is not too large or complex, people can adjust and then quickly adapt their movements to accurately perform the task. For instance, when reaching to a target with a misaligned hand cursor or after donning prism goggles, participants make large initial errors in their reaches, and with practice, errors initially reduce quite quickly, and then gradually reduce until returning to baseline levels (Krakauer et al., 2005; Krakauer et al., 1999; Sainburg & Wang, 2002). This learning curve can be observed for most types of learning (both skill acquisition and adaptation). Krakauer (2009) shows that when reaching to a single target with a hand cursor rotated 30°, people usually require 20 trials to return to previous baseline levels, or what he calls saturated or asymptotic levels. These adapted movements can be retained over several hours to several days, such that relearning the same visual perturbation later usually leads to a faster learning rate known as savings (Bock & Schneider, 2001; Caithness et al., 2004; Klassen et al., 2005; Krakauer, 2009; Krakauer et al., 2005; Krakauer et al., 1999; Tong & Flanagan, 2003).

Another measure of learning is known as aftereffects — a persistence of movement deviations when the distortion is removed that are consistent with movements produced during the distortion. In other words, if participants have adapted their movements, then they should persist in making these modified (adapted) movements after the perturbation is removed. In the case of adapting to a clockwise-rotated hand cursor, participants would continue to reach in a counterclockwise direction even when reaching either without a cursor or with a cursor that has been realigned with the hand, for at least a few more trials (Martin et al., 1996b; Redding, Rossetti, & Wallace, 2005). These aftereffects reflect an updated motor command and thus, an updated internal model (Krakauer, 2006; Simani et al., 2007).

The learning curves described above are visible when the perturbation (whether visual or dynamic, as with a force-field perturbation) is abruptly introduced. However, aftereffects arise either when the perturbation is abruptly or gradually (incrementally) introduced (Buch et al., 2003; Cressman, Salomonczyk, & Henriques, 2010; Klassen et al., 2005; Mattar, Darainy, & Ostry, 2013). For larger or more complex distortions, people tend to adapt more (i.e., show greater aftereffects) when these distortions are gradually introduced (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010; Kagerer, Contreras-Vidal, & Stelmach, 1997).

Proprioception

Proprioception provides the CNS with signals pertaining to the relative location of body parts with respect to each other. Proprioceptive information is derived from receptors in the muscles, joints, and skin (Augustine, 2008). The main receptors that provide proprioceptive information about limb position and motion are the afferent neurons that wrap themselves around muscle spindles (or intrafusal muscle fibers) located within the muscle body itself. The length of muscle spindles vary with the extrafusal muscle fibers that surround them and provide information about how much the limb is extended or flexed. Thus, muscle spindles provide continuous information about the limb’s relative location with respect to the rest of the body prior to, during, and after movement. To a lesser degree, Golgi tendon organs, joint receptors, and cutaneous or tactile receptors can also provide information about limb position. This somatosensory (proprioceptive and tactile) information enters the spinal cord via the dorsal column. Some of these sensory neurons innervate neurons within the spinal cord to provide input to spinal reflexive movements. Other sensory neurons travel up the spinal cord to S1 via the dorsal column-medial lemniscal system: This tract travels up the spinal cord, decussates in the medulla, and then continues to S1 through the thalamus.

For reach movements, the CNS uses this proprioceptive information to derive estimates of limb location and motion. In the PPC, this information is also combined with visual feedback of the hand and arm to produce a unified estimate of the limb (Culham et al., 2006; Culham & Valyear, 2006). When a discrepancy between vision and proprioception is large, changes in movements and in estimates of hand position arise. When perceptual estimates of hand position are altered due to a visual-proprioceptive mismatch of hand location following several reaches, we call this proprioceptive recalibration (Henriques & Cressman, 2012; Redding et al., 2005).

Proprioceptive Recalibration

As mentioned earlier, altering visual feedback of the hand leads to reach adaptation. However, recent studies also suggest that when participants repeatedly experience a discrepancy between where they see their hand represented and where it actually moves, not only do they adapt their reaches but also their sense of felt hand position shifts in the direction of the visual distortion. In other words, we call this process proprioceptive recalibration. The effect of reach training with altered visual feedback on hand proprioception has been explored with prism adaptation and more recently in virtual reality environments (Harris, 1965; Hay & Pick, 1966; Martin, Keating, Goodkin, Bastian,

& Thach, 1996a; Redding & Wallace, 2001; Simani et al., 2007; van Beers, Sittig, & Gon, 1999; van Beers, Wolpert, & Haggard, 2002). In a virtual reality experiment, Simani et al. (2007) observed that participants adapted their reaches to visual targets following training with a rightward translation of the reaching hand cursor. As previously observed in studies using prism adaptation (Redding & Wallace, 1988b, 2001; Rossetti et al., 1998; van Beers et al., 1999), participants showed aftereffects not only for visual targets, but proprioceptive and visual-proprioceptive targets as well. Simani and colleagues (2007) found that participants' errors made with their adapted and unadapted hands to different sensory targets were related in an additive manner. The researchers concluded that proprioceptive recalibration contributes to visuomotor adaptation.

However, many of the prism adaptation studies and virtual reality reach experiments that claim to find that visuomotor adaptation leads to proprioceptive recalibration tend to suffer from a confound. That is, these paradigms used adapted hand goal-directed reaches to assess proprioceptive changes, usually by having participants point to a site beyond the body midline or to their opposite, unadapted hand. Thus, the proprioceptive recalibration that these studies report may reflect the adapted motor command that arises because participants use the adapted arm to reach to non-visual goals. In response, our lab developed a perceptual paradigm for measuring hand proprioception that was designed to avoid this possible confound (Clayton, Cressman, & Henriques, 2013; Cressman & Henriques, 2010, 2012; Cressman et al., 2010; Mostafa, Salomonczyk, Cressman, & Henriques, 2014; Salomonczyk, Cressman, & Henriques, 2013;

Salomonczyk et al., 2012). Instead of having participants use their adapted arm to reach to different targets following reach training, we use a robot to guide the adapted hand to specific locations, and then have people make perceptual judgments regarding the location of their unseen hand. Specifically, participants either push the robot handle along a robot-generated path (active) or allow the robot to move their hand along the path (passive) (Cressman & Henriques, 2010). Once their hand arrives at the path's end, a reference marker appears or a beep sounds, and participants make a two-alternative forced-choice decision about their felt hand position relative to a visual reference marker or the body midline (Clayton et al., 2013; Cressman & Henriques, 2009; Jones, Cressman, & Henriques, 2010; Mostafa et al., 2014; Salomonczyk et al., 2013). We call this the proprioceptive estimation task. During these proprioceptive estimates, an adaptive staircase algorithm determines the hand's proximity to the reference marker, so that hand placement by the robot depends on the participants' previous response (Kestin, 1958; Treutwein, 1995). Using these responses, sense of felt-hand position at each reference location can be computed.

Regardless of active or passive hand placement in the proprioceptive estimation task, our lab has observed that participants show significant shifts in their sense of felt hand position in the direction of the visuomotor distortion. This recalibration is usually about 20% (6.1°) of the introduced visuomotor distortion, and thus about one third of the magnitude of the adapted movement, specifically the reach aftereffect produced without a cursor following training. The size of proprioceptive recalibration is similar across both visual reference marker and body-midline marker. Likewise, recalibration arose both after participants adapted to a cursor that was gradually rotated by 30^{o} or translated by 4 cm (Cressman & Henriques, 2009). However, abruptly introducing the 30^{o} cursor rotation leads to equivalent reach aftereffects and changes in felt position (Salomonczyk et al., 2012). They also found that (right-handed) participants who trained with the left or right hand produced similar shifts in perceived hand position for the trained hand, around 7.6°. A follow-up study by Mostafa et al. (2014) using a translated cursor showed similar results for the trained hands, but motor adaptation transferred from the dominant, trained (right) hand to the non-dominant, untrained (left) hand, and no intermanual transfer of proprioceptive recalibration was observed. Thus, proprioceptive recalibration arises only for the trained hand, and this change is unlikely to reflect some visual-spatial recalibration since, in that case, we would observe changes in both the trained and untrained hands. Cressman et al. (2010) also explored visuomotor adaptation and proprioceptive recalibration in older adults, and found young and older adults adapted their reaches and recalibrated their sense of felt hand position following rotated cursor training to an equal extent. Salomonczyk et al. (2011) explored the effect of both prolonged training and training with increasing rotation magnitudes on reach adaptation and proprioceptive recalibration. For the group that performed all three reach training sets (i.e., three sets of 99 trials to neighboring targets) with a 30° clockwise (CW) rotated hand cursor, their resulting reach aftereffects and proprioceptive recalibration did not increase with each additional training set but saturated at around 18° and 7° respectively. The group that experienced increasing magnitudes of cursor rotation (30°, 50°, 70°) across three training sets showed that larger rotations led to larger reach aftereffects and larger changes in felt hand position. These reach and proprioceptive changes were of similar proportions in that they were about 50% and 20% of the cursor rotation's magnitude. In sum, our lab has shown that proprioceptive recalibration of the hand is robust following different reach adaptation task combinations.

Other recent studies have also investigated how visuomotor adaptation influences sensory estimates of the hand using paradigms that avoid the motor confound in the earlier studies mentioned above. Synofzik, Linder, and Thier (2008) had cerebellar patients and healthy controls make self-directed hand movements with their right hand that could cross anywhere on a 90° arc while receiving rotated visual feedback of their reaching hand. In some trials, participants made these self-directed hand movements without a cursor or any visual feedback and were asked to indicate where their hand had crossed the arc (by moving another cursor to that site with their left, unadapted hand). Both patients and healthy individuals showed a significant shift in these estimates of unseen hand direction consistent with the visuomotor distortion, but patients' estimates were only half of the size of controls' estimates. Izawa, Criscimagna-Hemminger, and Shadmehr (2012) used a similar paradigm, except participants pointed with their unadapted hand to indicate the remembered location where their adapted hand had crossed a 90° arc in the workspace following reach adaptation to a gradually introduced 30° rotated cursor. Izawa et al. also found that both controls and cerebellar patients showed a significant change in their estimates of self-directed unseen movements of their adapted hand, although the change was again smaller for patients. In a paradigm more similar to that used in our lab but using a force-field adaptation, Ostry, Darainy, Mattar, Wong, and Gribble (2010) assessed participants’ sensed limb motion following adaptation to a velocity-dependent force-field by having a robot move their hand along a path that either veered to the left or to the right. Participants reported which direction they had felt the robot passively move their hand. Ostry et al. (2010) found that after force-field training, participants’ sense of limb movement was significantly shifted in the direction of force-field training, and this find was later replicated (Mattar et al., 2013). Thus, adapting reaching movements to a visual or force-field perturbation leads to somatosensory changes.

Proprioceptive recalibration has been shown in another type of training where volitional movement to targets is removed. In Cressman and Henriques (2010), instead of using the usual reach training, participants’ trained hand was passively moved toward a briefly presented target. In the main training condition, the cursor representing the hand always moved directly to the target site, but the accompanying hand motion gradually rotated 30° counter clockwise (CCW) around the home position while participants’ hands moved outwards. This paradigm allowed Cressman and Henriques to explore if exposure to a visual and proprioceptive discrepancy was enough to drive proprioceptive recalibration; there was neither unconstrained, volitional motion nor motor performance errors to drive adaptation and recalibration. They found that indeed, this discrepancy was sufficient to produce similar changes in estimates of hand position as found following the usual visuomotor adaptation training. This finding was replicated by Salomonczyk et al. (2013), but in that case, changes observed after reach training with larger cursor rotations (relative to the passively moved hand) saturated at a level found following training with a 30° visual-proprioceptive discrepancy. Thus, exposure to a visual and proprioceptive feedback discrepancy produces variable somatosensory changes that depend on how motions are executed and feedback is presented.

The aim of the current study is to determine how much of a discrepancy of hand position needs to be experienced in order for proprioceptive recalibration to occur. Here, we reverted back to the typical visuomotor adaptation paradigms. Instead of having a cursor present during the entire or most of the movement, the hand cursor appeared only at the hand movement's end during reach training with both an aligned and a rotated cursor.

Terminal Feedback

When adapting reach movements to altered visual feedback of the hand, the quality of visual information provided may affect the degree of motor learning. In experimental settings in which a cursor represents hand movements in a virtual reality environment, visual information can be manipulated to provide limited feedback. For example, the hand-cursor could appear only at the end of the reaching movement, which is referred to as terminal feedback (Cohen, 1967; van der Kooij, Brenner, van Beers, Schot, & Smeets, 2013) or knowledge of results (KR) (Hinder, Tresilian, Riek, & Carson, 2008; Shabbott & Sainburg, 2010; Sülzenbruck & Heuer, 2011); some researchers include entire hand path displays at a reach’s end when providing terminal feedback or KR (Bernier, Chua, & Franks, 2005; Shabbott & Sainburg, 2010; Sülzenbruck & Heuer, 2011). When visual feedback of the hand is limited, we tend to rely on other sources of information, including prior knowledge, to guide our reaches (Kording & Wolpert, 2004). In some cases (as we will describe in more detail below), terminal feedback may be as good as continuous feedback for inducing reach adaptation. However, other studies investigating reach adaptation following reach training with terminal feedback of a hand-cursor have shown poorer adaptation compared to continuous feedback training conditions.

The extent to which reach adaptation occurs following training with continuous versus terminal feedback may be attributed to the difficulty of the task (i.e., the size of the distortion), and the extent of reach training provided. Hinder et al. (2008) showed that after reaching with a 60° rotated cursor to radial targets using an isometric joystick, participants who were given terminal feedback of the cursor showed no aftereffects following training, while those given continuous feedback showed classic aftereffects (persistent deviated reaches after removing the distortion). Nonetheless, learning curves during reach training trials with the distortion were similar across terminal and continuous feedback conditions. In contrast, Bernier et al. (2005), who used a smaller and gradually introduced cursor-rotation for reaches to three proximal targets, found that average aftereffects were a bit larger for participants who received terminal feedback, where the entire path was shown after each reach, than for those who received continuous feedback. In fact, aftereffects for participants in the continuous feedback group decayed quickly back to baseline levels while aftereffects following terminal feedback remained robust. Shabbott and Sainburg (2010) had participants reach to 8 radial targets with continuous feedback or terminal feedback (KR), which included the entire hand path. Although both groups of participants showed reduced reach errors to a 30° rotated cursor relative to hand movement during training, those given terminal feedback showed minimal aftereffects (produced when the cursor became aligned with the hand again). In a more recent study by van der Kooij et al. (2013), participants reached to targets in 3D with visual feedback of the hand rotated 5° left or right relative to the cyclopean eye. While both rotated terminal and continuous feedback conditions affected reaching movements of the unseen hand following training, reach aftereffects were larger in the continuous feedback group. Moreover, the size of these aftereffects did not increase with additional sets of training, three sets of 56 reaches, for either visual feedback group. These somewhat conflicting findings may be due to how the distortion was introduced and aftereffects assessed, i.e., using no-cursor reaches versus re-aligned hand-cursor visual feedback. It seems that for more difficult visuomotor rotations (e.g., abruptly introduced distortions or large distortions), aftereffects following training with terminal feedback are either smaller than those with continuous feedback (Shabbott & Sainburg, 2010; van der Kooij et al., 2013) or non-existent (Hinder et al., 2008), but introducing the distortion gradually reverses this trend such that larger aftereffects are seen following reach training with terminal feedback (Bernier et al., 2005).

Perhaps it is not surprising that aftereffects following training with terminal feedback are typically smaller or non-existent when the hand-cursor rotation is abruptly introduced (Hinder et al., 2008; Shabbott & Sainburg, 2010; van der Kooij et al., 2013). Terminal feedback experiments aside, other studies have shown that motor learning may be greater when training with a gradually introduced visual perturbation compared to an abrupt perturbation. For instance, Kagerer et al. (1997) found greater motor retention following adaptation to a 90° rotation when its introduction was gradual compared to abrupt. Buch et al. (2003) also reported smaller aftereffects following gradual exposure to a similarly large 90° visuomotor rotation compared to abrupt exposure, but only for older adults. However, for smaller, 30° rotations, like those used by Klassen et al. (2005) and Salomonczyk et al. (2012), no differences were found in aftereffects following reach training with a gradual vs. abruptly introduced distortion. Taken together, these results suggest that advantages in learning observed with gradually introduced hand-cursor distortions are only observed if the perturbation is especially large, or perhaps more difficult. Since reduced visual feedback of the hand under terminal feedback conditions could make adaptation challenging, a gradually introduced distortion may reduce the differences in learning between terminal and continuous feedback conditions.

Our first aim was to investigate the influence of terminal versus continuous visual feedback on reach adaptation. Given that a gradually-introduced perturbation may reduce the learning differences between terminal and continuous feedback, we slowly introduced the cursor rotation over 40 trials. As well, we had participants perform several sets of reach training trials in order to look at the extent of reach adaptation across blocks of reach training trials, as it was unclear if and when reach adaptation under terminal feedback conditions would saturate. Participants performed similar sets of reach training trials as in our previous study (Salomonczyk et al., 2011), in which we investigated reach adaptation following training with continuous hand-cursor feedback. The similarities in the two paradigms allowed us to directly compare reach adaptation following terminal vs. continuous feedback of the hand.

In addition to determining the influence of terminal hand-cursor feedback on reach adaptation, we also examined how terminal feedback during reach training trials affected subsequent sense of felt hand position. Previous results from our lab and others have shown that adaptation to a visuomotor distortion leads to changes not only in hand movement, but also to our sense of hand position or hand motion estimates. Specifically, we have previously found that when participants adapt their reaches to misaligned visual feedback of their hand, both their no-cursor reaches (i.e., post-training reaches without visual feedback used to assess reach adaptation), and their reaching hand's felt position change in a direction consistent with the visual perturbation (Cressman & Henriques, 2009; Cressman & Henriques, 2012; Cressman et al., 2010; Henriques & Cressman, 2012; Salomonczyk et al., 2011). Moreover, Synofzik et al. (2008) found that after participants adapted to rotated hand-cursor feedback, their sense of a previously produced reach movement shifted in the direction of the visual perturbation. Synofzik et al. (2008) asked healthy controls and cerebellar patients to reach with a cursor that was rotated 30°, and then afterwards to indicate the direction of their unseen hand movement, using a mouse-cursor controlled by their opposite hand. Controls misperceived the direction of this unseen movement in the direction of the visual perturbation, although patients did not. In Izawa et al. (2012), healthy participants and cerebellar patients localized the direction by which their unseen right hand had moved following reach training with a gradually introduced 30° rotated cursor, using their unadapted left hand. Both controls and patients showed comparable changes in reaching movements (specifically aftereffects) following training with the rotated cursor. However, compared to controls, patients showed significant but smaller shifts in their estimates of their unseen hand movements, or what Izawa et al. (2012) called the predictive consequences of these unseen hand movements. In addition to seeing changes in felt hand position or the predictive consequences of one's movements following training with a visuomotor distortion, Ostry et al. (2010) found that participants reported a shift in sensed limb motion after adapting their reaches to a velocity dependent force-field. Specifically, participants shifted their sense of limb motion in the direction opposite the force-field. In brief, sense of hand position or motion is altered in healthy participants following reach training with a visual or a dynamic perturbation.

In previous studies investigating changes in felt hand position or motion, the hand-cursor was continuously visible during the reach training trials. In contrast to these findings, we expect that terminal feedback – although perhaps sufficient to drive reach adaptation – may not induce sizeable proprioceptive recalibration, since participants see their rotated hand-cursor only at reach endpoint. Thus, the second aim of this study was to investigate whether terminal feedback of the hand when reaching with a visuomotor rotation was sufficient to lead to changes in felt hand position.

In this study, we determined changes in reaches and felt hand position after training with terminal hand-cursor feedback and compared these changes to changes observed in a previous study in which participants trained with continuous visual feedback of the hand (Salomonczyk et al., 2011). Our goal was to investigate both the extent of reach adaptation and changes in felt hand position following terminal feedback training. Secondary to this was to determine how much terminal feedback training was required for each of the changes to saturate and potentially achieve levels similar to those seen after continuous feedback training. Specifically, we measured reaching errors and proprioceptive estimates following each of three sets of 99 reach training trials and compared the results to Salomonczyk et al. (2011).

Hypothesis and prediction

Given that the terminal feedback of the hand greatly reduces the exposure to the discrepancy between visual and proprioceptive feedback during training known to drive both reach adaptation and proprioceptive recalibration, we expected that compared to continuous feedback such changes would be smaller, and may require additional training.

Methods

Participants

Eleven healthy, right-handed adults (mean age = 20.73, SD = 4.45, 7 female) were recruited from York University and volunteered to participate in the current experiment. Prior to participation, participants were prescreened for self-reported handedness and history of visual, neurological and/or motor dysfunction or injury. In addition to these participants, the results of ten participants (mean age = 21.5, SD = 2.62, 5 female) from a previous study (Salomonczyk et al., 2011) were included to serve as a control for comparing the quality of visual feedback on reach adaptation and proprioceptive recalibration. All participants provided informed consent prior to participating in accordance with the ethical guidelines of York University Human Participants Review Sub-committee.

Apparatus

Figure 2(A) provides a side view of the experimental set-up for the current and previous study. Participants were seated in a height-adjustable chair in order that they could comfortably view and reach to all targets and reference markers presented on an opaque, reflective surface while grasping the vertical handle of a two-joint robot manipulandum (Interactive Motion Technologies) with their right hand. The position of the robot handle was recorded at a sampling rate of 50Hz and had a spatial accuracy of 0.1 mm.

Installed 17 cm above the robot arm was a reflective surface onto which visual stimuli were projected from a LCD monitor (Samsung 510N, refresh rate 72Hz). The reflective surface was positioned so that targets and reference markers projected onto the surface appeared to lie in the same horizontal plane as the unseen robot manipulandum. All natural light was blocked from the room, the room lights were dimmed, and participants' view of their right hand and the manipulandum was occluded by the reflective surface and a black cloth that covered their right shoulder to the reflective surface.

General Procedure

To determine the effect of visual feedback quality on reach adaptation and changes in proprioceptive sense of hand position, we had participants reach to targets with terminal visual feedback of their hand position, and compared their performance with participants who had previously participated in a similar study in which continuous visual feedback of the hand was provided (Salomonczyk et al., 2011). For the terminal feedback group, during reach training trials, participants were only shown the hand-cursor at the end of their ballistic reach movements, while participants in the continuous feedback group were first shown the hand-cursor after the hand had travelled 4 cm from the home position toward the target (located 10 cm from the home position), up until the cursor acquired the visible target.

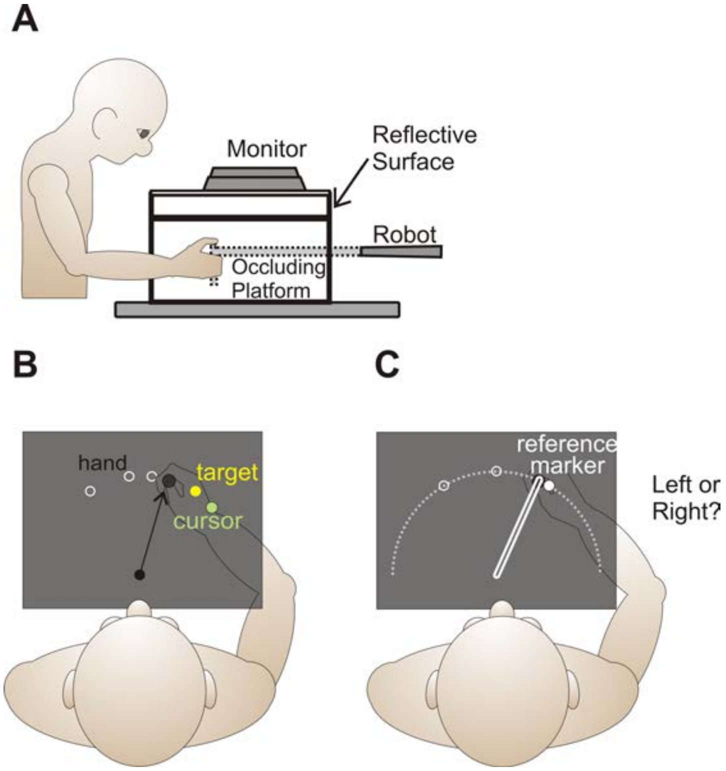

Figure 2: Experimental setup and design. Side (A) and top (B-C) view of experimental setup. (B) For both reaching training trials and no-cursor trials, reach targets, 1cm in size, (white rings) were located 10 cm from the home position (shown as a black circle), and were located 5° and 30° left and right of the body midline. In reach training trials, visual feedback of the unseen hand was provided by displaying a green cursor at the end of an initial reach in order that participants could obtain the target. During the first rotated training block, the green cursor, representing the hand, was gradually rotated to 30° clockwise, and remained at this magnitude for the rest of the task and throughout the remaining two blocks. (C) Hand-proprioceptive estimate task. Trials started from a home position, which was illuminated by a 1 cm dot for 500 msec. After the home position disappeared, participants pushed their hand out along a robot-guided constrained linear path (white rectangle on right) to a location on the white arc (not shown to participants) relative to 1 of 3 possible reference markers (white circles) 10 cm from the home position. The reference markers, which appeared only after the hand had finished its outward movement, were 1cm in diameter and located at 0° and 30° left and right of the body midline. Participants were required to indicate if their hand was left or right of the reference marker.

Following the reach training tasks, both groups then reached to the same targets without any hand-cursor feedback and performed a proprioceptive estimation task. Both groups performed two different testing sessions on two separate days (Table. 1). For session one, reaching training trials involved a cursor that was aligned with the unseen reaching hand to provide baseline measures of performance. For session two, the cursor was rotated during reach training trials, and the reach training, no-cursor reaches and proprioceptive estimate tasks were repeated three times in succession.

Task 1: Reach Training

In the reach training task (Fig. 2B and Table 3, Boxes 1, 3, and 5), participants reached to a visual target (yellow circle, 1 cm in diameter) from the home position using the robot manipulandum. Four reach targets were radially located 10 cm from the home position: 30° counterclockwise (CCW), 30° CW, 5° CCW and 5° CW of the body's midline (Fig 2(B)). Visual feedback was provided in the form of a hand-cursor (green circle, 1 cm in diameter) that indicated the reach end position (terminal feedback). The cursor was aligned with the actual hand position in the first testing session (Table 1) and gradually rotated to 30° CW relative to hand position during the first block of the second testing session. Participants began their reaches from a home position that was approximately 40 cm in front of them and aligned with their body midline. The home position was not illuminated during reach training trials. At the end of each reach trial, visual

Block Type	**Day 1**	**Day 2***	**Tasks**	**Trials**	**Special Notes**
1. Reach Training	Aligned Feedback	Misaligned Feedback	Reach Training	99 (3/target)	
2. Reach Training	Aligned Feedback	Misaligned Feedback	No-cursor Reaches	12 (4/target)	
3. Proprioceptive Estimate + Reach Training	Aligned Feedback	Misaligned Feedback	Reach Training	12 (4/target)	
4. Proprioceptive Estimate + Reach Training	Aligned Feedback	Misaligned Feedback	Proprioceptive Estimates	15 (5/marker)	Repeat 10 times: Tasks 4 and 5 prior to *No-cursor reaches*
5. Proprioceptive Estimate + Reach Training	Aligned Feedback	Misaligned Feedback	Reach Training	6 (2/target)	
6. Proprioceptive Estimate + Reach Training	Aligned Feedback	Misaligned Feedback	No-cursor Reaches	15 (3/target)	

Table 1 Order of the tasks completed in the two testing sessions. Each session was completed on separate days. (Session 1: Top Row) In the first testing session, participants reached to targets with terminal hand-cursor feedback such that the cursor was aligned with the hand (Box 1). This reach training was followed by no-cursor reach trials (Box 2). Afterwards, proprioceptive estimate trials were interleaved with further reach-training trials. This sequence was repeated a total of 10 times (Boxes 4-5). The session ended with another set of no-cursor reach trials (Box 6). (Session 2: Bottom Row) In the second testing session, the tasks (Boxes 1-6) were similar to that in Day 1, except the terminal cursor feedback was gradually rotated 30° CW from their actual hand position, reaching its full rotation of 30° by the 41st trial, and remaining at this rotation for the remainder of the trials (Box 1) and subsequent reach training trials (Box 3 and 5). These tasks (Boxes 1-6) constitute one block, and were repeated twice more for a total of three blocks.

**Note:* Reach Training block followed by Proprioceptive Estimate + Reach Training was repeated 3 times on Day 2.

feedback was eliminated, and participants returned their hand to the home position along a robot-established linear route (similar to Salomonczyk et al. (2011)). If participants attempted to move outside this linear route or grooved wall, a resistance force was generated (proportional to the depth of penetration with a stiffness of 2N/mm and a visual damping of 5N/(mm/s)) perpendicular to the grooved wall (also in (Cressman & Henriques, 2009; Cressman & Henriques, 2010; Cressman et al., 2010; Henriques & Soechting, 2003; Jones et al., 2010)). Trial order was pseudo–randomized such that participants reached to each of the two peripheral targets and one of two of the peri-central targets prior to any target repeating. Participants completed one set of 99 reach trials with the aligned-cursor in the first testing session (Table 1, Box 1) and three sets of 99 reach trials with the rotated-cursor in the second training session (Table 1, see note). In the first set of the rotated reach training trials, the cursor rotation was gradually introduced by rotating the cursor 0.75° CW relative to the hand each trial, until the maximum rotation of 30° CW was achieved on the 41st trial. This 30° CW rotation was maintained for all subsequent reach training.

During reach training trials with terminal feedback, the hand-cursor was not illuminated until the initial reach movement was complete, i.e., when the velocity of the hand was less than or equal to 3mm/sec for 0.5 sec. At this point, the hand-cursor appeared in order to provide participants with a visual representation of their hand location relative to the target at the end of their initial ballistic motion. After the hand-cursor appeared, participants were told to move the illuminated hand-cursor to the visible target, and the trial ended when the hand-cursor’s center and the target’s center were within 0.5cm of each other. In the infrequent case when participants managed to obtain the target in the first ballistic motion, the trial ended immediately: No visual feedback was provided from the hand-cursor, the target disappeared, and participants returned their hand to the position along a robot-generated, linear route. In contrast, for participants training with continuous feedback, the hand-cursor was first displayed once the hand had moved 4 cm from home position. The hand-cursor then remained visible until participants acquired the target (Salomonczyk et al., 2011). Thus, participants who experienced continuous visual feedback experienced real-time feedback about their unseen hand’s position in the workspace during their first ballistic motion.

Prior to the reach training task in the first testing session, participants in the terminal feedback group were given a practice session of 20 reach training trials with the aligned hand-cursor visible during the entire reach so that participants could become accustomed to the apparatus and reach task prior to introducing terminal visual feedback. In the continuous feedback condition, there were no preceding practice trials.

Task 2: No-cursor reaching

In the no-cursor reaching task (Table 1, Boxes 2 and 6), participants reached to the same visible targets but without visual feedback of the hand-cursor. After participants held their end position for 0.5 sec, the target disappeared, and participants’ hands were again guided back to the home position by a linear grooved path. We calculated reach aftereffects, by subtracting reach endpoints made without a cursor after aligned-cursor training (top row) from those produced after rotated-cursor training (bottom row). Participants reached to four visual targets three times (Box 2), and to the same four targets plus one addition target at 0° (i.e., body midline or center) following proprioceptive estimate trials with interleaved reach training (Box 6). This second set of no-cursor trials was to assess whether the aftereffects, and thus, reach adaptation decreased or decayed during the proprioceptive estimate test described below.

Task 3: Proprioceptive estimates

Proprioceptive estimate trials (Table 1, Box 4) began with participants holding their hand at the home position. The home position, indicated by a green, 1 cm diameter circle, was illuminated for 0.5 sec. After the home position disappeared, participants were instructed to push their hand outward along a robot-constrained, 10 cm long, linear path (Fig. 2(C), elongated rectangle). When a participant's hand arrived at the end of the path, a reference marker (yellow, 1 cm-diameter circle) appeared. Participants were instructed to make a two-alternative forced-choice decision regarding whether they felt that their unseen hand was left or right of this reference marker. Following their response, participants returned their hand to the start position using the same robot-generated, linear path and began the next trial. The reference markers were located 30° CCW, 30° CW or 0° relative to the body midline (Fig. 2(C), white and open circles). Participants' hand position relative to each reference marker was adjusted over the course of 50 trials using an adaptive staircase algorithm (Kestin, 1958; Treutwein, 1995), as previously described in our other studies (Cressman & Henriques, 2009; Cressman & Henriques, 2010; Jones et al., 2010; Salomonczyk et al., 2011). As in Salomonczyk et al. (2011), there were two staircases per reference marker, each starting at 20° either left (CCW) or right (CW) of the reference marker (Fig. 3). As outlined by Cressman and Henriques (2009), the two staircases were adjusted individually and randomly interleaved.

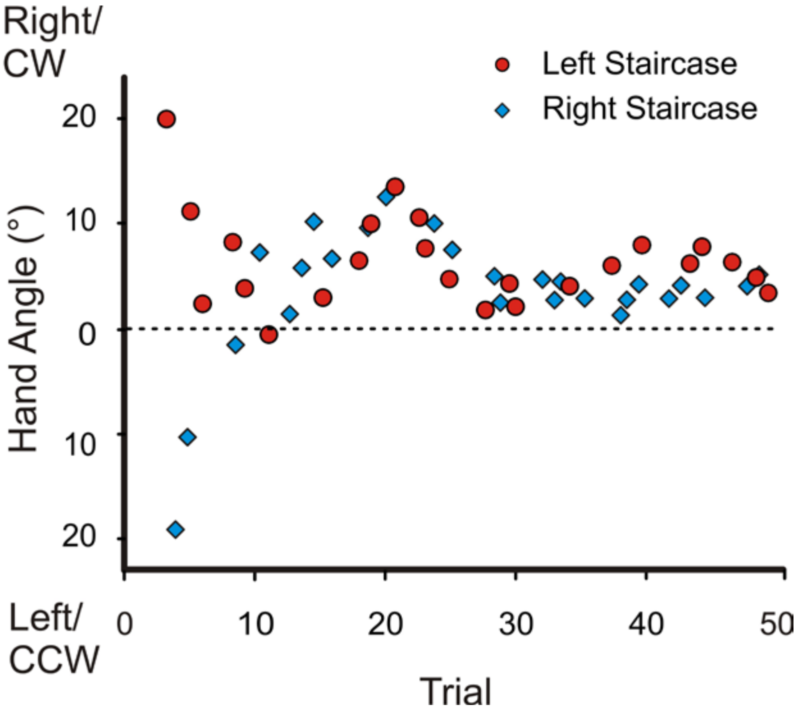

Figure 3: Angular hand position during proprioceptive estimate trials. The left and right staircases began with a participant's hand placed 20° from either side of the reference marker (dotted line). These adaptive staircases progressively converged over successive trials.

Proprioceptive estimate trials were interleaved with reaching-training trials (Table 1, Boxes 4-5). Fifteen proprioceptive estimate trials and 6 reach training trials (with either an aligned or rotated cursor) immediately followed these initial reach training trials (Table 1, Boxes 4-5). A set of 15 proprioceptive estimate trials and 6 reach training trials was completed 10 times, and then participants performed 15 no-cursor reaching trials. Thus, there were a total of 150 proprioceptive estimate trials per block.

Testing Sessions: Aligned and misaligned blocks

The three aforementioned tasks were arranged in blocks within testing sessions that were completed on two days, between 24 hours to 30 days apart. Each block consisted of 99 trials of reach training (Table 1, Box 1), no-cursor reaches (Box 2), proprioceptive estimate trials intermixed with further reach training trials (Boxes 3-5), and ended with a second set of no-cursor (aftereffect) reaches (Box 6). Only one block was completed in the first testing session, where the cursor was aligned with the hand in reach training trials, and the no-cursor reach errors and proprioceptive estimates served as a baseline for future rotated-cursor blocks. The second day of testing consisted of three blocks which were performed in succession, as it was unknown whether reach adaptation or shifts in felt hand position following training with terminal feedback would be evident after only one block, (as was the case for continuous feedback) or would require a second or third block of training. Moreover, it was unclear if these changes would increase in size with each set of reach training. The testing sessions were identical to those in the continuous visual feedback study (Salomonczyk et al., 2011).

Data Analysis

Reaches: Motor Adaptation

Our main analysis was to determine if open-loop reach errors (i.e., aftereffects) following rotated-cursor training differed from those following aligned-cursor training and if aftereffects following each set of 99 trials with the rotated cursor differed from one another. We also compared these differences or aftereffects across the two sets of no-cursor reaches within each block (epoch 1 and epoch 2) to determine if the aftereffects decayed following proprioceptive estimates interleaved with reaching training. To examine reach errors, we analyzed the endpoint angle errors and the angle of the hand at peak velocity (PV) in the no-cursor reach trials. Endpoint errors were defined as the angular difference between a movement vector (the linear path from the home position to movement endpoint) and the reference vector (the linear path joining the home position to the target). PV angle was defined as the difference in angle between a movement vector, which joined the home position to the point at which the hand reached peak velocity, and the reference vector. For both endpoint errors and angle at peak velocity (PV), we conducted a 4 block (aligned 1 vs. rotated 1 vs. rotated 2 vs. rotated 3) by 2 epoch (post-reach training vs. post-proprioceptive estimates with interleaved reaching) by 4 target location (30° left vs. 30° right vs. 5° left vs. 5° right) RM-ANOVAs for the terminal feedback group. In order to determine if additional training with rotated terminal feedback yielded any increase in aftereffects over successive blocks, we calculated reach aftereffects by subtracting the no-cursor reaches for the aligned block from each of those of the three rotated blocks, and then ran another 3-way ANOVA but this time with only three blocks (rotated 1-3). Likewise, we used reach aftereffects to compare these changes in movements for the terminal feedback and continuous feedback group, using a mixed ANOVA with visual feedback type (terminal versus continuous) as a between-participants factor and block (rotated 1 vs. rotated 2 vs. rotated 3) and epoch (post-reach training vs. post-proprioceptive estimates with interleaved reaching) as within participants factors.

Proprioceptive estimates of hand position

We examined the influence of training with terminal hand-cursor visual feedback on proprioceptive estimates of hand position. For each participant, we fit a logistic function to his or her responses for each reference marker (Fig. 4). From the logistic function we determined the participant's bias, which is an estimate of the participant's accuracy of their sense of felt hand position (Cressman & Henriques, 2009; Cressman & Henriques, 2010). Bias is represented by the point at which participants responded "left" (and "right") 50% of the time (Cressman & Henriques, 2009; Cressman & Henriques, 2010; Jones et al., 2010; Salomonczyk et al., 2011). We compared these estimates of felt hand location relative to reference markers after aligned-cursor training (baseline) with those after misaligned-cursor training.

Bias was analyzed in a 4 block (aligned 1 vs. rotated block 1 vs. rotated block 2 vs. rotated block 3) by 3 reference marker location (30° CCW, 0°, 30° CW) RM-ANOVA. This was followed by another ANOVA where we compared the changes in sense of felt hand position across additional rotated-training blocks by subtracting biases from the aligned session from those biases measured following each rotated set, so that the number of training blocks was reduced to three. These changes were then compared to changes in sense of felt hand position following reach training with continuous visual feedback of the hand in a 2 by 3 mixed ANOVA with visual feedback type (terminal and continuous) as a between-participants factor and block as a within participants factor.

For all ANOVAs, differences with a probability of less than .05 were considered significant and pairwise comparisons were Bonferroni corrected. We report Greenhouse-Geisser corrected p-values when required.

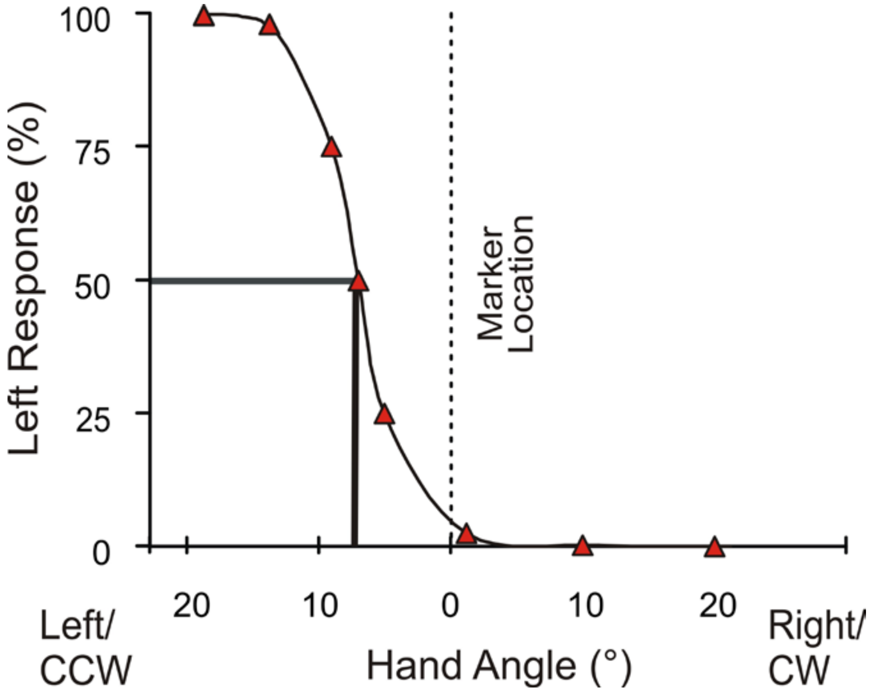

Figure 4: Percentage of left responses for the 0° visual reference marker for a single person. A logistic function was fitted to a representative participant's data to define bias, where bias is the probability of responding left 50% of the time.

Results

Motor adaptation

Participants reached to targets with an average movement time of 1.2 s ± .3 s (SD) and an average peak velocity of 15.9 cm/s ± 9.5 cm/s (SD) in the no-cursor reaches. In Salomonczyk et al. (2011), the average movement time was 1.95 s ± .93 s (SD) and the average peak velocity was 16.4 cm/s ± 5.9 cm/s (SD). Mean reach endpoint errors for trials performed after aligned-cursor training were 3.7° to the right of the target. These open-loop reaching errors (prior to adaptation) indicate that participants were moderately accurate with their reaches to targets even when they lacked visual feedback pertaining to their hand position. These reach errors were a bit more shifted than those observed in the continuous feedback study: in our previous study, these errors were 0.75° to the right of the target (Salomonczyk et al., 2011).

We compared these open-loop reaches following training with an aligned cursor with those following rotated-cursor training and found a substantial shift in the direction that participants reached after training with both terminal and continuous feedback, as shown in Fig. 5. For terminal feedback training, the no-cursor reaches deviated significantly leftwards compared to the reaches following the aligned-cursor training block, $F(3,30) = 36.97$, $p < .001$, and this was true following all three blocks of rotated-cursor training: aligned cursor block - rotated cursor block: rotated block 1 = 14.1° ($p <. 001$); rotated block 2 = 12.1° ($p < .001$); rotated block 3 = 11.8° ($p = .001$). The no-cursor reaches relative to baseline (i.e., reach aftereffects) for the terminal feedback group (Fig. 5, pink squares) were slightly smaller, by roughly 5.8° across rotated blocks than those found for the continuous feedback group (green squares), $F(1,19) = 4.5$, $p = .047$. As reported in Salomonczyk et al. (2011), the no-cursor reaches were also significantly different between the aligned block and the three rotated blocks when participants used continuous feedback. We also found that further rotated training with terminal feedback (the additional 2 blocks) did not lead to substantially larger aftereffects, $F(2,20) = 2.21$, $p = .136$. The same was true for participants receiving continuous feedback (Salomonczyk et al., 2011) (Fig. 5, green squares).

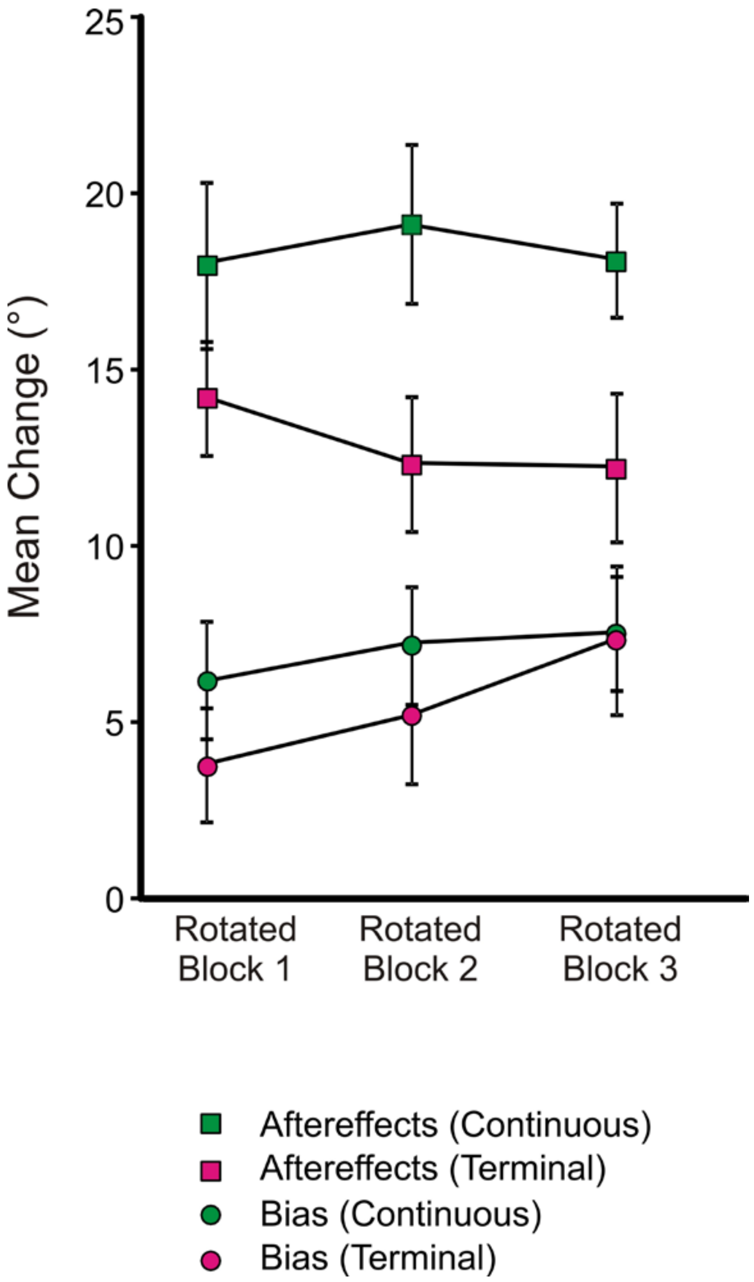

Figure 5: Angular changes in endpoint angle of reach aftereffects and proprioceptive biases. Angular changes in endpoint angle of reach aftereffects and proprioceptive biases across the three blocks of rotated reach training relative to performance in the first testing session with the aligned hand-cursor. Pink symbols indicate mean performance from the terminal feedback experiment while green symbols represent those from the continuous feedback experiment (Salomonczyk et al., 2011). Mean changes in degrees were averaged across participants and across target/reference marker locations. Error bars represent standard error of the mean.

When we compared the terminal feedback aftereffects (i.e., change in no-cursor reaches relative to baseline performance) made soon after reach training (epoch 1) with the aftereffects completed after proprioceptive estimates (epoch 2), we found no significant difference across the three blocks $F(1,10) = 1.67$, $p = .22$. Likewise, no changes in epoch were found for the continuous feedback group (Salomonczyk et al., 2011). Thus, participants reached with similar errors before and after completing the proprioceptive estimate trials.

We found a similar pattern of results for changes in the angular reach deviation at PV, as we did for the angular endpoint errors described above for the terminal feedback group. Directional errors at peak velocity were significantly more leftward following all rotated reach training blocks compared to the aligned training block, ($F(1.461, 14.609) = 19.16$, $p < .001$), in that all comparisons of these no-cursor reaches between the aligned training block and each of the three rotated blocks were significantly different ($p < 0.01$). When comparing reach aftereffects, for the most part, the angular deviations at PV closely resembled those of the endpoints (within 2°) for the terminal feedback group. This was different than the continuous feedback group, where the angle at PV deviated from the endpoint error by 5°, suggesting that these open–loop reaches were much straighter in the terminal feedback group than in the continuous feedback group. Overall, there was no change over rotated training blocks, thus additional rotated training had no significant impact on PV angle.

Bias

Next, we wanted to determine if adapting to a rotated cursor with terminal feedback also led to similar changes in felt hand position, i.e., proprioceptive recalibration, as has been seen after training with continuous visual feedback of the hand-cursor. Figure 6(A) displays the three reference marker locations (circles), average biases following aligned-cursor training (diamonds) and rotated-cursor training (triangles) when terminal feedback was provided. Each successively darker triangle represents participants' estimates of felt hand position relative to the reference marker for rotated blocks 1, 2 and 3. Figure 6(B) uses the same schematic to illustrate the results under continuous feedback conditions (Salomonczyk et al., 2011). In the terminal feedback condition, for the aligned block, felt hand locations were slightly left of the reference markers, specifically 7.3° left of the reference marker. This leftward bias has been previously observed in our lab and is due to a hand bias (Jones et al., 2010); this hand bias was also observed in the continuous feedback condition (Salomonczyk et al., 2011), where the average bias across participants and reference markers for the aligned block was 5.1° leftward.

For terminal feedback, we see that each rotated block yielded estimates of felt hand locations that were successively further left of the reference markers and the estimates after training with an aligned hand-cursor, consistent with the direction of the visuomotor distortion (Fig. 5, pink circles). There was a main effect of training block among the aligned and three rotated training blocks, $F(3,30) = 8.62$, $p < .001$. Thus, we next assessed whether biases after each

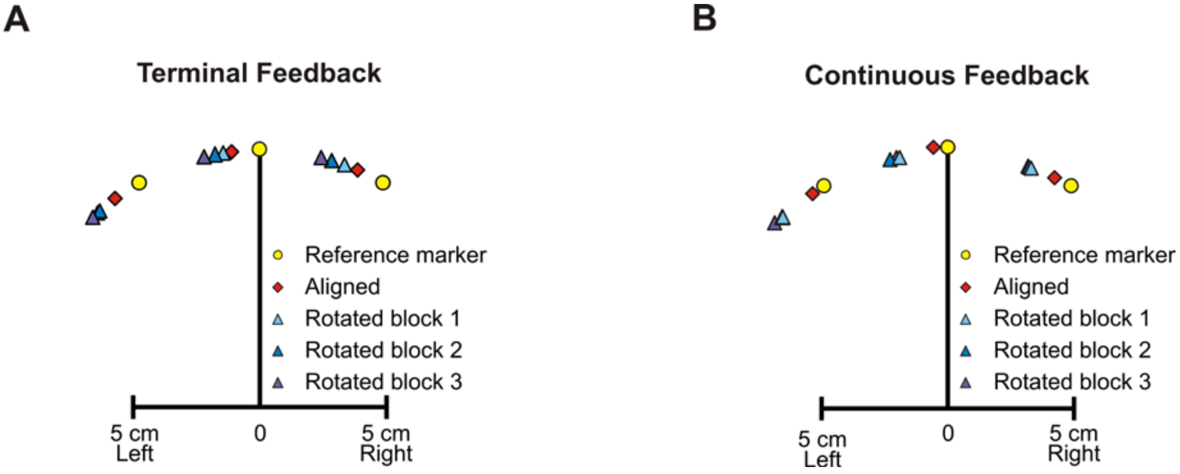

Figure 6: Mean 2-D proprioceptive biases for the terminal feedback experiment (A) and continuous feedback experiment (B) (Adapted from Salomonczyk et al., 2011). Participants estimated their hand position relative to reference markers (yellow circles) following aligned hand-cursor feedback training (red diamonds) and rotated hand-cursor training (first rotated block: light blue triangles: second rotated block: dark blue triangles; third rotated block: purple triangles).

rotated set were significantly shifted relative to those following the aligned-cursor training. We found that although biases were not shifted for the first rotated block, they were for the second and third rotated blocks relative to the aligned block: rotated block 1 - aligned, 3.4° (*p* = .404); rotated block 2 - aligned, 5.1° (*p* = .035); rotated block 3 - aligned, 7.4° (*p* = .008). Additionally, the change was much larger, by 4°, in the last rotated block compared to the first rotated block (*p* = .029), suggesting that more practice with terminal feedback led to greater proprioceptive recalibration (illustrated by the increasing height of the pink circles across blocks in Fig. 5). This was not the case for the continuous feedback group (Salomonczyk et al., 2011), where the significant change in bias saturated after the first set of rotated training (Fig. 5, green circles).

Interestingly, we found that the overall size of the change in felt hand position was similar across the terminal and continuous feedback groups, in that there was no significant difference in changes in bias for the terminal feedback and continuous feedback groups, $F(1,19) = 0.56$, $p = .46$. Although Salomonczyk et al. (2011) did not find a significant difference across the three blocks of rotated training, when we looked at the change in bias across the three rotated blocks for the terminal feedback group, we found that they did significantly differ as explained above. Thus, both feedback groups reached a similar level of change in felt hand position by the end of the three training blocks.

Motor adaptation and proprioceptive recalibration

To better compare changes in reaches (aftereffects) to changes in felt hand position, we ran a linear regression to see whether changes in felt hand position depended on changes in reach aftereffects. As consistent with our previous studies (Cressman & Henriques, 2009; Salomonczyk et al., 2011, 2013; Salomonczyk et al., 2012), we found no significant relationship between the changes ($p = 0.17$, $R^2 = 0.06$), although as usual the change in felt hand position was much smaller than the reaching aftereffects for the two feedback groups (Fig. 5). More importantly, we found that despite significantly smaller reach aftereffects following terminal feedback training, compared to continuous feedback training, the overall change in felt hand position was similar between the two feedback groups, at least by the third block. Again, this suggests that the sensory changes are not directly related to motor changes.

Discussion

The present study had two goals: to explore the effect of terminal visual feedback on reach adaptation compared to continuous visual feedback, and to examine whether terminal feedback experienced during reach training affects our subsequent estimates of felt hand position. Participants reached to three targets for a total of 99 trials with visual feedback of their hand rotated 30° clockwise relative to hand movement, in three blocks. After each training set of 99 trials, participants reached to the same targets without a cursor, and then estimated the position of their trained, unseen hand relative to reference markers at similar locations. On average, we found that participants who experienced terminal visual feedback both adapted their reaches and recalibrated their felt hand position. Mean reach aftereffects approached 13° after the first rotated block, and were maintained at that level even after two additional training blocks. Sense of felt hand position was also recalibrated by 3.4° after the first training block, however, changes in felt hand position increased further and significantly to 7.41° by the third reach training block. Compared to participants who experienced continuous feedback, participants experiencing terminal feedback appeared to adapt their reaches less (by about 33%) over the three training blocks, but their sense of felt hand position, although initially shifted less than participants in the continuous feedback group, reached a comparable level by the third training block.

Role of visual feedback quality in reach adaptation

In the current study, we provided three sets of reach training trials in order to determine how long it takes for reach adaptation to saturate when terminal feedback is provided (by the end of the third training set, participants had reached to each of the proximal targets 99 times). Surprisingly, our extra training trials did not lead to increased aftereffects over successive training blocks. Aftereffects following the first 99 training trials were not significantly different from those found after the last 99 trials (reach adaptation equal to ~13°). This is similar to the results of including extra training with a continuously visible rotated cursor in the comparison study, which also included the same targets and same three training blocks (reach adaptation equal to ~18.44°; (Salomonczyk et al., 2011)). This was also seen in an earlier study of ours (Wong & Henriques, 2009), where we had participants reach with a rotated cursor to similar targets for at least 200 trials each day for 5 consecutive days. Thus, increased training neither helped nor decreased the discrepancy in the extent of motor learning between terminal and continuous feedback conditions. Also, terminal feedback resulted in smaller aftereffects, compared to continuous feedback. This difference was not due to decay over the open-loop reach trials, since aftereffects were constant within a block.

Unlike some of the studies mentioned in the introduction, we found substantial and significant aftereffects. Studies that did not show sizable aftereffects after reaching with terminal feedback either displayed the entire hand path after each reach and/or measured their aftereffects by re-introducing an aligned cursor during aftereffect reaches (Hinder et al., 2008; Shabbott & Sainburg, 2010) or imposed a much larger rotation (abrupt 60° versus our gradual 30°; (Hinder et al., 2008)). The exception is Bernier et al. (2005) who oddly showed that aftereffects following training with continuous feedback washed out quickly compared to aftereffects following training with KR, which were initially large and did not washout. Like us, they also gradually introduced the visual perturbation, and had participants reach 80 times to each of three nearby targets. The other terminal feedback study that used a small rotation (van der Kooij et al., 2013) showed results similar to ours. Their reaching results, or what they called realignment of the unseen hand, showed significant changes in open-loop reaches following terminal feedback, and these changes were about one third smaller than those produced by participants who trained with continuous feedback. Aftereffects in our study showed a similar one-third difference between those produced after training with terminal versus continuous feedback.

A key difference between our study and the others reported is that we gradually introduced the rotated hand-cursor. Except for Bernier et al. (2005), other terminal feedback studies introduced the cursor rotation abruptly (Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Hinder et al., 2008; Shabbott & Sainburg, 2010). Previously, we have shown that after training with continuous feedback there is no difference in aftereffects regardless of whether the 30° cursor rotation was introduced gradually or abruptly (Salomonczyk et al., 2012).

Moreover, abrupt and gradual rotated training has led to equivalent learning retention a day later (Klassen et al., 2005). However, it is possible that in poorer visual feedback conditions, there may be differences in reach aftereffects. We know that when the cursor rotation is particularly large (e.g., 90°), people generate greater aftereffects when the perturbation is introduced gradually compared to when the perturbation is abrupt [(Buch et al., 2003; Kagerer et al., 1997) *N.B.* Buch et al. (2003) only found this for their older participant group]. Thus, how a visual perturbation is introduced may impact learning only in the case of more challenging perturbations. As such, with terminal feedback, participants may have benefited from the gradually-introduced rotation in our study, which may explain why we found significant aftereffects in the present study.

Since terminal feedback does not allow for on-line corrections during the reach, it is possible this absence may have led to poorer learning, or no learning at all. In our task, we allowed for on-line corrections by having the hand-cursor become visible at the end of the ballistic component of each reach and requiring participants to move the hand-cursor to the target to end the trial. Tseng, Diedrichsen, Krakauer, Shadmehr, and Bastian (2007) compared reach adaptation, and the resulting aftereffects, in trials between participants who were permitted to make on-line corrections at a movement’s end with another group of participants who were not allowed to make on-line corrections (with a continuously visible cursor). They found that adaptation rates and aftereffects were not different between these two conditions. Thus, we do not expect that the post-reach motion to the target had a significant impact on reach aftereffects in our terminal feedback task.

The effect of training with terminal feedback on hand proprioception

Few studies have assessed hand proprioception alongside reach adaptation. In our study, we derived participants’ sense of felt hand position with a task that does not require goal-directed reaches, by asking participants to report the location of their (robot-guided) felt hand position relative to a reference marker (Clayton et al., 2013; Cressman & Henriques, 2011; Cressman & Henriques, 2010; Cressman et al., 2010; Mostafa et al., 2014; Salomonczyk et al., 2011, 2013; Salomonczyk et al., 2012). We found that participants recalibrated their felt hand position following rotated hand-cursor training, even after adapting with only terminal altered feedback of their hand. However, this proprioceptive shift only achieved significance after the second block of training, and continued to increase in size during the third and final block. By this final block of rotated terminal feedback training, participants’ shift in felt hand position was comparable to shifts in felt hand position experienced by participants in the continuous feedback condition. With continuous feedback, Salomonczyk et al. (2011) found that additional training, beyond the first block of 99 trials, did not lead to further recalibration following a 30° rotation, however gradually increasing the cursor rotation (up to 70°) did lead to larger changes in felt hand position (as well as reach aftereffects). This change in felt hand position following rotated continuous feedback training was similar whether the cursor was gradually or abruptly introduced (Salomonczyk et al., 2012). It is unknown whether introducing the terminal misaligned cursor abruptly would have a similar effect on proprioceptive recalibration.

Independence of reach adaptation and proprioceptive recalibration

Our results, along with those from prior studies from our lab and others, suggest that changes in reaches and changes in felt hand position following training with altered visual feedback of the hand are independent of each other. First, the point in training by which maximum changes were achieved was different for the two measures. As with the results for continuous rotated feedback, (Salomonczyk et al., 2011), we also found no significant correlation between the changes in reaches and hand proprioception. Results from related studies in our lab have also shown this lack of correlation; and more convincingly, some show different patterns of generalization for reach aftereffects and changes in hand proprioception (Mostafa et al., 2014). Results from other labs testing patients with cerebellum damage also suggest this independence of motor and sensory changes following training with a rotated cursor. In Izawa et al. (2012), while cerebellar patients adapted their reaches to a perturbation that was gradually introduced to the same extent as controls (similar reach aftereffects), patients showed smaller changes in what the authors called the predictive consequences of unseen hand movements; these were measured by having participants reach with their unadapted hand, to the location at which they perceived their unseen adapted had previously moved (Izawa et al., 2012).

Moreover, Synofzik et al. (2008) found that while cerebellar patients did not learn to adapt their reaches to a cursor rotation that increased by 6° per trial (i.e. somewhat abruptly) as well as controls, they did recalibrate their estimates of their arm movements. However, similar to Izawa and colleagues (2012), this recalibration seen in the patients was less than in the controls. In brief, the pattern of changes in motor adaptation and proprioceptive recalibration following training with terminal feedback add to the argument for motor adaptation and sensory recalibration’s independence.

Conclusion

Following visuomotor adaptation using terminal visual feedback, participants adapted their reaches and recalibrated their sense of felt hand position, but these changes were smaller than those for participants who received continuous visual feedback. Based on the present study, we suggest that terminal feedback provides sufficient information for motor learning, even after only 99 trials (33 trials per target). But, while motor adaptation remained relatively stable after the first rotated training block, additional training was necessary for attaining maximal changes in felt hand position. We suggest that the current terminal feedback paradigm provides further evidence for the relationship between motor learning and sensory recalibration processes, two processes that change concurrently, yet independently.

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Appendix A

Informed Consent Form (for unpaid participants)
Date:

Study Name: Multisensory interaction in motor control and learning

Researchers: Dr. Denise Henriques

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 3 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. Denise Henriques either by telephone at (416) 736-2100, extension 77215 or by e-mail (deniseh@yorku.ca). 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 416-736-5914 or e-mail ore@yorku.ca).

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