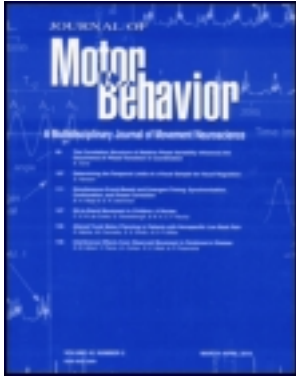


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REVIEW ARTICLE

Visuomotor Adaptation and Proprioceptive Recalibration

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ABSTRACT. Motor learning, in particular motor adaptation, is driven by information from multiple senses. For example, when arm control is faulty, vision, touch, and proprioception can all report on the arm's movements and help guide the adjustments necessary for correcting motor error. In recent years we have learned a lot about how the brain integrates information from multiple senses for the purpose of perception. However, less is known about how multisensory data guide motor learning. Most models of, and studies on, motor learning focus almost exclusively on the ensuing changes in motor performance without exploring the implications on sensory plasticity. Nor do they consider how discrepancies in sensory information (e.g., vision and proprioception) related to hand position may affect motor learning. Here, we discuss research from our lab and others that shows how motor learning paradigms affect proprioceptive estimates of hand position, and how even the mere discrepancy between visual and proprioceptive feedback can affect learning and plasticity. Our results suggest that sensorimotor learning mechanisms do not exclusively rely on motor plasticity and motor memory, and that sensory plasticity, in particular proprioceptive recalibration, plays a unique and important role in motor learning.

Keywords: motor learning, multisensory, reaching, plasticity

One approach to studying motor learning involves investigating or simulating adaptation of well-learned movements (e.g., saccades and reaches to visual targets) in the context of various perturbations. These perturbations include altered visual feedback of the hand or target (generally known as visuomotor adaptation training), or applying static and dynamic forces on the hand during goal-directed arm movements. In this review, we mainly discuss studies on and models of visuomotor adaptation on reaching movements, and then explore not only the effect of this type of learning on motor performance, but also on sensory estimates of the effector.

The dominant influence of vision on motor learning has been demonstrated by numerous studies examining visuomotor adaptation. In these studies, participants reach to a target while their hand location is visually misrepresented, for example, by having participants wear laterally displacing prism goggles or when the hand is hidden from view and a cursor on a screen represents the hand as being shifted left of its actual position. If the shift is relatively small or introduced gradually, participants tend not to notice the perturbation, and they reduce these cursor-to-target errors by adapting their limb movements (Abeele & Bock, 2001; Flanagan & Rao, 1995; Ghahramani, Wolpert, & Jordan, 1996; Krakauer, 2009; Mazzoni & Krakauer, 2006; Sainburg & Wang, 2002; van den Dobbelen, Brenner, & Smeets, 2004; Vetter, Goodbody, & Wolpert, 1999; Werner & Bock, 2007; Wolpert, Ghahramani, & Jordan, 1995). For example, when participants reach

toward a leftward target but the cursor representing their hand veers left from the initial start position, they adjust the direction of their reaching movement to the right so that the cursor moves to the target. Moreover, these movements continue to deviate when reaching in the dark without visual feedback. These persistent reaching deviations, known as aftereffects, demonstrate that a new representation or sensorimotor mapping has been learned, and are considered to be a measure of the extent of motor learning. Visuomotor learning is considered to be acquired implicitly, as providing participants with explicit instructions does not facilitate learning and in fact can impede it (Mazzoni & Krakauer, 2006).

Most studies on, and models of, motor learning, focus almost exclusively on these ensuing changes in motor performance without exploring the implications on sensory plasticity, that is whether the sensory estimates of hand position change following learning. Given that adapting to visuomotor distortions comprises not only a discrepancy between one's desired movement and the actual movement produced, but also a discrepancy between the seen and felt position of the reaching hand, it seems plausible that learning to reach with altered visual feedback of the hand may result in sensory plasticity. While models of motor learning incorporate error signals that reflect the difference between predicted sensory estimates and actual sensory feedback of the movement, these models tend to assume either a unified state estimate of the hand-effector, or a state estimate based on vision. Yet, how visual and proprioceptive signals are integrated (e.g., the relative weight assigned to each sensory modality), has been shown to be flexible, such that sensory weighting changes depending on the stage of movement planning (Sober & Sabes, 2003, 2005), target position (van Beers, Sittig, & Denier van der Gon, 1996, 1998, 1999; van Beers, Sittig, & Gon, 1999), and target modality (Sarlegna & Sainburg, 2007; Sober & Sabes, 2005). Moreover, these computations for state estimation could depend on how the information is to be used. Visually guided movements may involve placing more weight on visual feedback (or even predicting the visual location of the limb when vision is absent) than would a task that merely involves localizing the hand in the absence of vision (Mon-Williams & Bingham, 2007; Sober & Sabes, 2005). While many studies have examined how these different sensory signals are integrated, few studies have focused on whether these sometimes conflicting sensory inputs affect or recalibrate each other (what we refer to as

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cross-sensory recalibration). It is possible that vision merely overrules other sensory estimates like those from proprioception when it is available, but does not recalibrate them or lead to any persistent change in proprioception after vision is removed (Smeets, van den Dobbelen, de Grave, van Beers, & Brenner, 2006). This question is the focus of the present article.

In general, it is assumed that sensorimotor adaptation relies mainly on error-based learning (Berniker & Kording, 2008; Hinder, Riek, Tresilian, de Ruyg, & Carson, 2010; Shadmehr, Smith, & Krakauer, 2010; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Wei & Kording, 2009), although other non-error or model-free signals such as use-dependent plasticity and operant reinforcement have recently been shown to contribute to some aspects of motor performance as well (Diedrichsen, White, Newman, & Lally, 2010; Huang, Haith, Mazzone, & Krakauer, 2011). That is, motor adaptation involves either reducing the difference between an individual's desired performance and actual performance, or between the predicted and actual sensory consequences of an individual's movements. Specifically, if the seen hand movement does not reach the desired goal or differs from the predicted outcome, then the brain uses these errors to change motor performance on subsequent movements. In this review we suggest a second error signal that depends not so much on motor error or error in the predicted sensory consequences of movements, but on the error or discrepancy between sensory estimates of limb position, specifically those of vision and proprioception. We propose that this cross-sensory error signal contributes to both reach adaptation and changes in perceived hand position (as we describe subsequently), neither of which can be explained by conventional error-based learning, nor by present models of sensorimotor learning. This hypothesis is based on recent results from our lab that suggest that sensorimotor learning not only leads to changes in movements (what we call motor recalibration) but also to changes in perception of hand position (Cressman & Henriques, 2009; Cressman, Salomonczyk, & Henriques, 2010; Salomonczyk, Cressman, & Henriques, 2011), although not hand path geometry (T. Wong & Henriques, 2008). Even more importantly, our findings suggest that changes in movements may arise in part due to this sensory recalibration (Cressman & Henriques, 2010).

We are not the first to suggest that visuomotor learning leads to proprioceptive recalibration or what is sometimes known as proprioceptive realignment or sensory remapping. In fact, many researchers investigating adaptation of reaching movements to displacing prisms have suggested that visuomotor adaptation and resulting aftereffects arise in part due to participants recalibrating their sense of felt hand position to match their seen hand position (Craske & Gregg, 1966; Harris, 1963, 1965; Hay & Pick, 1966; Redding & Wallace, 1978, 1988, 1996, 1997, 2001, 2002, 2003, 2006; Templeton, Howard, & Wilkinson, 1974). This hypothesis is based on studies that have shown that reaches made to proprioceptive targets following training to reach to visual

targets while wearing laterally displacing prism are similarly deviated, although not all studies show this effect (e.g., Bernier, Gauthier, & Blouin, 2007). In this case, the proprioceptive target is usually a position in space perceived to be aligned with body midline (Harris, 1963, 1965; Hay & Pick, 1966; Redding & Wallace, 1978) or participants' unadapted hand (Craske & Gregg, 1966; Harris, 1965). Both visual and proprioceptive recalibration processes are proposed to arise slowly, after an initial strategic (cognitive) stage in which an individual attempts to quickly reduce his or her performance errors when reaching with prisms (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2011; Redding & Wallace, 1996, 2001, 2002, 2006). Yet, it is these slow spatial recalibration processes that lead to a realignment of visual and proprioceptive reference frames and thus, reach aftereffect errors (Redding, Rossetti, & Wallace, 2005).

While the prism literature discusses sensory recalibration processes and suggests a role for them with respect to motor adaptation, it is difficult to interpret the sensory shifts outlined above as providing direct evidence of sensory recalibration. First, prism adaptation paradigms typically show only the final view of the hand or end-effectors (in some cases projectiles thrown at the target; Martin, Greger, Norris, & Thach, 2001; Martin, Keating, Goodkin, Bastian, & Thach, 1996a, 1996b). This is because seeing initial hand position along with the target, even a displaced view, would enable participants to use vision to plan the correct movement vector and hence does not lead to motor aftereffects or sensory recalibration (Redding & Wallace, 1996). Second, given that prisms also shift the view of the target and the rest of the workspace, it is unclear whether changes in goal-directed arm movements, made either to visual reach training targets or proprioceptive targets, are due to how the brain assigns the source of such errors (as opposed to sensory recalibration), which has been shown to have implications on motor learning (Berniker & Kording, 2008; Clower & Boussaoud, 2000). Finally, changes in the straight-ahead reaching task (or other reaching tasks used to assess proprioceptive recalibration) could reflect participants' utilizing their adapted motor commands (Hatada, Miall, & Rossetti, 2006). Thus, some of the sensory changes observed following reaches with prisms could arise due to motor adaptation or because of a spatial realignment of the workspace rather than to recalibration in the sensory system(s).

It is only recently that intersensory recalibration arising from reaching with distorted visual feedback of the hand in a virtual reality environment has begun to be explored (Simani, McGuire, & Sabes, 2007; van Beers, Wolpert, & Haggard, 2002). In contrast to the prism literature discussed previously, reaching in a virtual reality environment has the advantage of allowing the experimenter to shift only the location of the seen hand, as opposed to the entire workspace, hence avoiding any possible visual recalibration. Initial work in this area by Simani et al. had participants adapt their reaching movements to visual targets in response to a virtually shifted view of the hand (a cursor), and then measured their subsequent

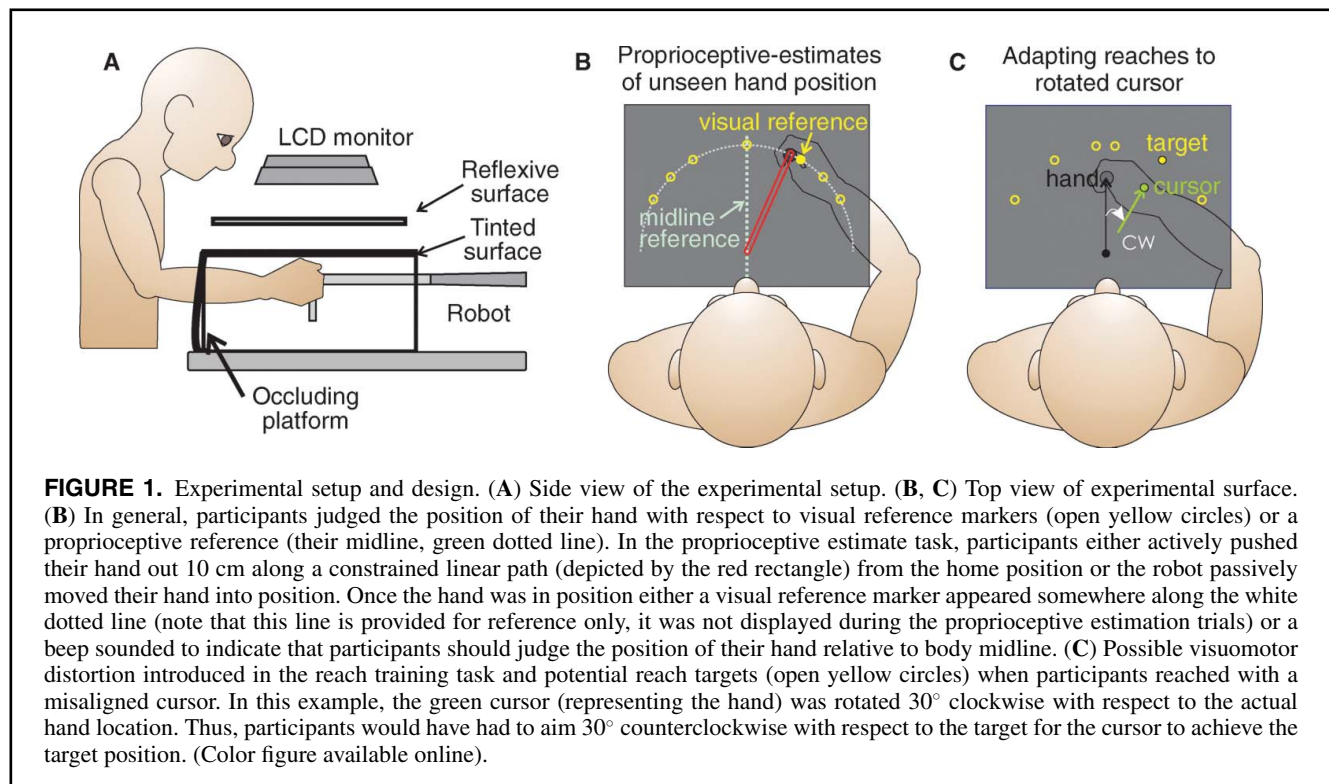
reaches to both visual and proprioceptive targets with both hands. In accordance with results from the prism literature discussed previously, learning to reach with the translated hand–cursor led to systematic changes in the subsequent open-loop reaches that were additive. The authors interpreted these linearly related reaching aftereffects as indicating that the motor adaptation observed resulted from intersensory recalibration. However, it is unclear if their results just reflect intersensory recalibration per se since, like in many other studies exploring sensory plasticity, Simani et al. required participants to make voluntary reaching movements to assess proprioception, using the same arm that was adapted. Thus, it is unclear whether changes in these proprioceptive measures are really due to proprioceptive recalibration or motor recalibration (i.e., a change in the motor command or the motor representation). After all, generalization of motor adaptation has been shown to account for changes in reaching in the various tasks that Simani et al. used to assess sensory recalibration (e.g., examining performance at a novel target location and with the opposite [untrained] hand; Berniker & Kording, 2008).

In order to determine the extent that such adapted movements are sensory based versus motor based, we have developed an innovative method of measuring hand proprioception that avoids active target-directed movements. Using our technique, we can better establish important differences in sensory and motor plasticity, and better understand the role of cross-sensory recalibration in motor learning. Subsequently we describe our novel technique for

measuring hand proprioception and then explain how we use this unbiased measure of proprioception to investigate sensory and motor recalibration in motor learning.

Measuring Hand Proprioception

To measure participants' proprioceptive sense of hand position (Cressman & Henriques, 2009, 2010; Cressman et al., 2010; Jones, Cressman, & Henriques, 2009; Salomonczyk et al., 2011), we used a two-joint robot manipulandum (Figure 1A) to precisely place or guide the participant's hand to specified locations in the workspace. Once the hand was in the required position, participants were required to judge whether their unseen hand was located to the left or right of either a visual reference marker or their body midline (Figure 1B). Importantly, the reference marker appeared only once the hand has arrived at its final location, so it could not serve as a target of any sort. The location of the hand relative to this visual or proprioceptive (body midline) reference was adjusted by an adaptive staircase algorithm across 50 trials for each reference marker according to participants' responses. We then used these two-alternative forced choice responses to map out each participant's sensitivity function for each reference marker location within the workspace, and calculated a proprioceptive estimate of hand position for each of these locations (yellow circles in Figures 1B and 2A). We then determined whether these estimates of hand position change (become displaced or less precise) as a result of learning to reach with a misaligned cursor. When we compared



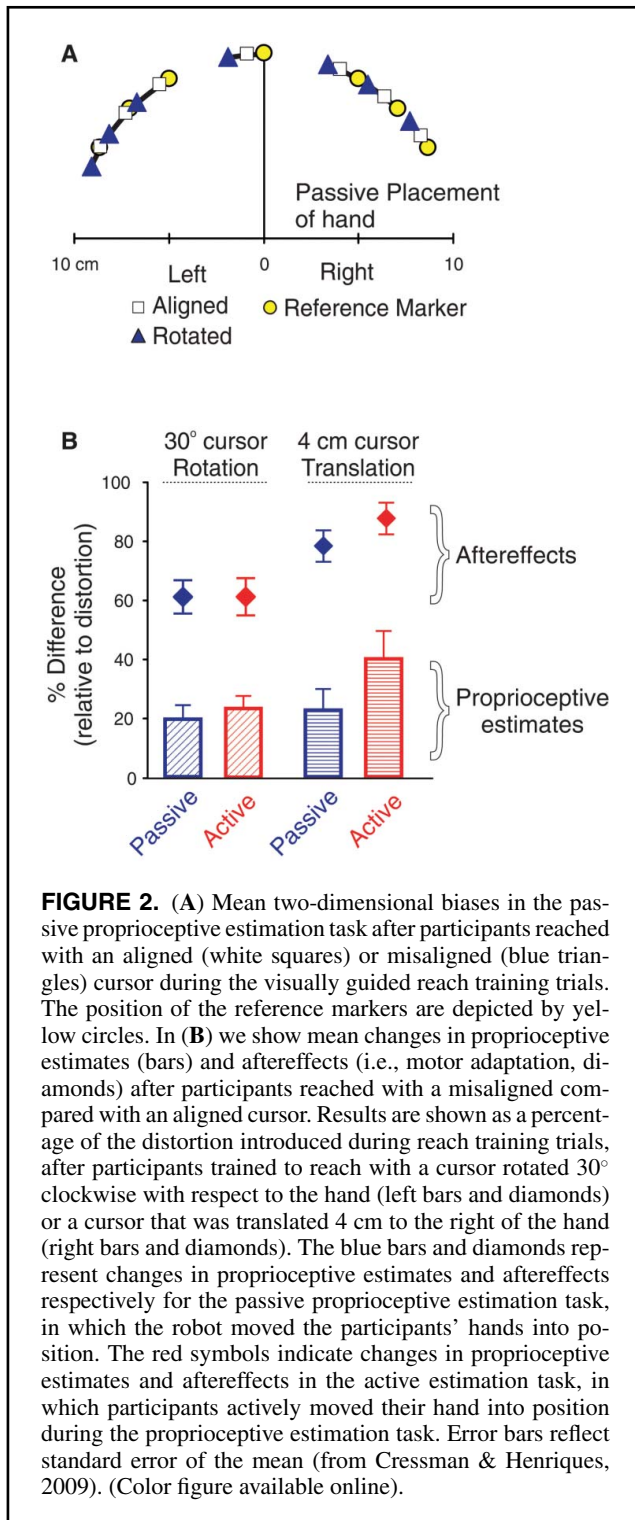


FIGURE 2. (A) Mean two-dimensional biases in the passive proprioceptive estimation task after participants reached with an aligned (white squares) or misaligned (blue triangles) cursor during the visually guided reach training trials. The position of the reference markers are depicted by yellow circles. In (B) we show mean changes in proprioceptive estimates (bars) and aftereffects (i.e., motor adaptation, diamonds) after participants reached with a misaligned compared with an aligned cursor. Results are shown as a percentage of the distortion introduced during reach training trials, after participants trained to reach with a cursor rotated 30° clockwise with respect to the hand (left bars and diamonds) or a cursor that was translated 4 cm to the right of the hand (right bars and diamonds). The blue bars and diamonds represent changes in proprioceptive estimates and aftereffects respectively for the passive proprioceptive estimation task, in which the robot moved the participants' hands into position. The red symbols indicate changes in proprioceptive estimates and aftereffects in the active estimation task, in which participants actively moved their hand into position during the proprioceptive estimation task. Error bars reflect standard error of the mean (from Cressman & Henriques, 2009). (Color figure available online).

this method of assessing hand proprioceptive sensitivity with more typical methods, we found these perceptual estimates of right hand position were just as accurate and precise as endpoints achieved when participants reproduced their felt hand movement and even more precise and accurate than reaches made by the opposite hand (Jones et al., 2009; Jones & Hen-

riques, 2010). Recently, Ostry, Darainy, Mattar, Wong, and Gribble (2010); Wilson, Wong, and Gribble (2010); and J. D. Wong, Wilson, and Gribble (2011) used a similar procedure for measuring hand proprioception that also involves using a two-joint robot to guide participants' hands. Participants then judge either the direction by which the hand deviates along a specified path or how a test location differs in direction compared to a previous reference hand location.

In general, we find that participants show a significant change in their proprioceptive sense of hand position following adaptation to a visuomotor distortion. Prior to adaptation, participants tend to misestimate their right unseen hand (white squares in Figure 2A) as being several degrees to the left or counterclockwise (CCW) of the reference marker locations (yellow circles). This slight leftward bias appears to be a consistent misestimate of the position of the right hand; estimates of the unseen left hand (not shown) tend to fall to the right (Jones et al., 2009; Wilson et al., 2010). More importantly, following adaptation (to a hand–cursor distortion in which the cursor is gradually rotated 30° clockwise [CW] relative to hand position in the case of Figure 2A and as shown in Figure 1C), the proprioceptive estimates of hand position (blue triangles) are further shifted CCW or left and thus in the direction of the visual feedback during training with the misaligned cursor (Cressman & Henriques, 2009; Cressman et al., 2010; Salomonczyk et al., 2011). That is, participants misestimate the location of their adapted unseen hand as being closer to where they saw the cursor representing their hand during the visuomotor adaptation trials.

We found that this change in proprioceptive estimates was about 6° following adaptation to a 30° visuomotor rotation, or about 0.8 cm following adaptation to a 4 cm visuomotor (lateral) translation, which represents about 20% of the magnitude of the cursor distortion introduced as illustrated in Figure 2B. Thus, the relative magnitude of change in felt hand position was the same across the two different types of distortions, although aftereffects were proportionally larger after adapting to the lateral displacement perturbation compared to the rotation (diamonds on the right are higher than those on the left in Figure 2B). Likewise, this recalibration of hand proprioception was the same whether these measurements were made on trials in which participants actively moved their hand out along a robot force-generated slot or channel (active proprioceptive estimation task: red bars in Figure 2B) or the robot passively moved the hand into position (passive proprioceptive estimation task: blue bars). When we increased the size of the visuomotor rotation (e.g., the cursor was gradually rotated by 30°, then 50°, then 70° before measuring hand proprioception each time), the resulting shifts in proprioceptive estimates of the hand also increased (bars in Figure 3A). Nonetheless, the shift was always proportional to the size of the distortion, representing about 20% of the magnitude of the hand–cursor distortion (Figure 3B). Moreover while aftereffects also increased in size as a function of the magnitude of the distortion (diamonds in Figure 3A), there was no correlation between the relative changes in

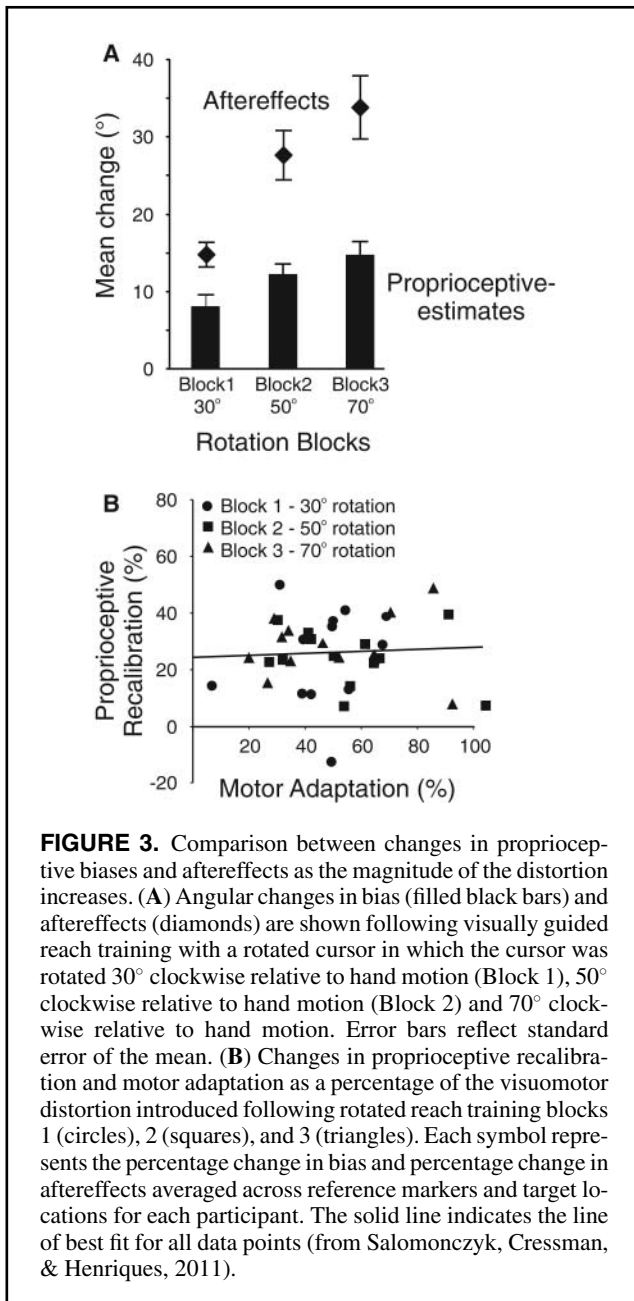


FIGURE 3. Comparison between changes in proprioceptive biases and aftereffects as the magnitude of the distortion increases. **(A)** Angular changes in bias (filled black bars) and aftereffects (diamonds) are shown following visually guided reach training with a rotated cursor in which the cursor was rotated 30° clockwise relative to hand motion (Block 1), 50° clockwise relative to hand motion (Block 2) and 70° clockwise relative to hand motion. Error bars reflect standard error of the mean. **(B)** Changes in proprioceptive recalibration and motor adaptation as a percentage of the visuomotor distortion introduced following rotated reach training blocks 1 (circles), 2 (squares), and 3 (triangles). Each symbol represents the percentage change in bias and percentage change in aftereffects averaged across reference markers and target locations for each participant. The solid line indicates the line of best fit for all data points (from Salomonczyk, Cressman, & Henriques, 2011).

proprioception and that of the aftereffects (Figure 3B). In accordance with our findings, Ostry et al. (2010) found a significant, but somewhat smaller, magnitude of change in felt hand position following force field adaptation: shifts of 11% of the estimated magnitude of learning (based on peak deviations in aftereffects). In our studies described previously, the magnitude of proprioceptive changes observed were greater than 33% of the size of aftereffects following adaptation to a visuomotor rotation and translation, for the various distortion sizes tested. This difference between changes in hand position estimates following adaptation to a velocity dependent force field compared with that of a visuomotor distortion likely arises due to the latter introducing a discrepancy be-

tween proprioceptive and visual feedback of hand location while force perturbations do not (Sarlegna & Bernier, 2010).

In summary, we have shown that this change in felt hand position following adaptation is consistent across various parameters, including (a) distortion (i.e., rotation [30° CW] vs. lateral displacement [4 cm] of hand cursor), (b) how the hand position is achieved (i.e., whether participants actively move their hand out along a robot force-generated slot or channel compared with when the robot passively moves the hand into position for the proprioceptive estimate trials; Figure 2B), and (c) the magnitude of the distortion. We have also found similar changes in proprioceptive estimates of hand position regardless of (d) reference marker location, (e) how the distortion is introduced (gradual vs. abrupt visuomotor rotation), (f) the number of reach training trials completed prior to the proprioceptive estimate trials, (g) age, and (h) the hand (left or right) used to make the estimates (following adaptation of the same tested hand; Cressman & Henriques, 2009; Cressman et al., 2010; Salomonczyk et al., 2011). Finally, we have shown shifts in felt hand position when participants judge the position of their hand relative to both visual and proprioceptive (body midline) reference markers. Given this shift in felt hand position across reference marker modalities and the fact that we did not find any transfer of sensory shifts to the opposite hand (i.e., adapting one hand did not lead to changes in proprioceptive estimates of the opposite hand), suggests that the shifts in estimates of hand position we are measuring are a change in proprioception as opposed to merely some visual recalibration or realignment between visual and proprioceptive space (Cressman & Henriques, 2011; Salomonczyk, Cressman, & Henriques, 2010).

This recalibration of felt hand position seems to require that there be a sufficient discrepancy between visual and proprioceptive feedback regarding hand position. Specifically, merely reaching to targets with veridical visual feedback of the hand does not lead to changes in subsequent movements made to the same visual targets with the unseen hand, as shown by Smeets et al. (2006). Similarly, when comparing results of two of our studies using the same participants, we also found that proprioceptive estimates of hand position were no different after reaching 125 times to visual targets with an aligned cursor, than those measured without this preceding reach training; this was the case both for passive displacement of the hand and active displacement of the hand during the proprioceptive estimation task (Cressman & Henriques, 2009; Jones et al., 2009). However, we did find that proprioceptive sensitivity was greater (i.e., the uncertainty range was smaller) after this reaching practice, but only for measurements when the hand was passively displaced during the estimation task (shaded bars compared with white bars in Figure 4A) and not the actively displaced task (Figure 4B). J. D. Wong et al. (2011) recently investigated the role of aligned reach training on proprioceptive estimates more explicitly. They measured sensitivity of proprioceptive estimates of the passively displaced hand (specifically

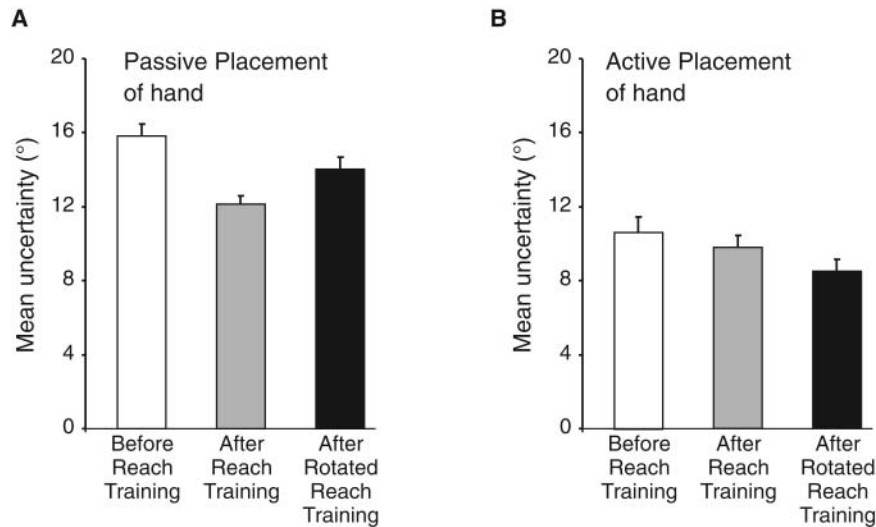


FIGURE 4. Magnitude of the uncertainty ranges in the proprioceptive estimation tasks averaged across reference marker positions and participants prior to reach training (white bars), following reach training with a veridical cursor (shaded grey bars) or with a rotated cursor (black bars) when the robot passively moved participants' hands into position (**A**, passive proprioceptive estimation task) and when participants actively moved their hands into position (**B**, active proprioceptive estimation task). Error bars reflect standard error of the mean (from Cressman & Henriques, 2009; Jones, Cressman, & Henriques, 2010).

the uncertainty range) either in the same workspace as where participants practiced reaching to targets with a veridical cursor for 10 min, or in a novel workspace. Results indicated that the sensitivity of passively placed hand positions were only reduced in areas that participants had practice reaching in. They, similar to us, found no differences in the felt position of the hand (what we refer to as proprioceptive bias), which is consistent with the results of Smeets et al. However, this consistent absence of recalibration of proprioceptive estimates of hand position following training with veridical visual feedback of the hand could just be a matter of degree. As discussed previously, proprioceptive recalibration tends to be roughly 20% of the size of the discrepancy between vision and proprioception. It could be that the natural discrepancy between our visual and proprioceptive estimates of hand position is small enough that a 20% change is not detectable.

Sensory Versus Motor Plasticity

Another important aspect of this sensory plasticity that we have observed is that changes in felt hand position do not correlate with motor aftereffects (Figure 3B) in any of our studies involving visuomotor adaptation. That is, although adaptation to a visuomotor distortion leads to changes in sensory estimates of hand position and changes in open-loop movements, larger aftereffects didn't consistently lead to larger proprioceptive shifts. This suggests that sensory and motor plasticity may be the result of separate processes or mechanisms involved in responding to altered visual feedback of the hand, rather than causally linked. For example, differences

between proprioceptive and motor recalibration may be the result of different error signals, each driving distinct changes in the nervous system's representation of the body and the world. It has been shown that differences in assigning credit to or estimating the source of motor errors can explain different rates of motor learning (Smith, Ghazizadeh, & Shadmehr, 2006) and generalization of this learning across various conditions (Berniker & Kording, 2008). The CNS needs to attribute movement errors to specific changes in the body or the world, or both, likely using Bayesian inferences, before determining the necessary corrections (source-estimation model; Berniker & Kording). Of course, there are many ways in which a representation or internal model of the body or the world could be incorrect and thus different systems (e.g., sensory and motor systems) could be influenced by different error signals (simultaneously) during motor learning (Wei & Kording, 2009), as a result of assigning credit to different sources. That is, in the same way that the Berniker and Kording source-estimation model attributes motor errors to the most probable source(s) of this error, such a model could also account for independent changes in hand proprioception based on different error signals (including this cross-sensory discrepancy).

In accordance with the suggestion that proprioceptive recalibration and motor adaptation are independent processes, visuomotor adaptation has been demonstrated in the absence and degradation of proprioceptive input. For example, deaf-fingered individuals have been shown to adapt their reaches in response to altered visual feedback of the hand (Bernier, Chua, Bard, & Franks, 2006; Ingram et al., 2000; Miall &

Cole, 2007). As well, it has recently been demonstrated that healthy subjects adapt their movements in response to a visuomotor distortion even when proprioceptive feedback is degraded by agonist-antagonist muscle vibration (Bock & Thomas, 2011; Pipereit, Bock, & Vercher, 2006). These findings suggest that motor and sensory changes could be driven by different error signals and that part of the adaptive process, when proprioceptive information is available, may be to reduce conflicting sensory information.

In attempt to better investigate this difference in sensory and motor plasticity following adaptation to altered visual feedback of the hand, and the role of cross-sensory discrepancy in motor learning, we devised a learning paradigm that isolated the visual-proprioceptive discrepancy from the usual visuomotor discrepancy (Cressman & Henriques, 2010). In this learning or training paradigm, participants were exposed to a discrepancy between visual and proprioceptive feedback of their hand position, but were not allowed to make any volitional, free-reaching movements with this false visual feedback. Instead, the robot either moved (passive hand motion task) or guided (active hand motion task) their unseen hand toward a briefly presented target. Participants always saw the hand–cursor move directly to the target site, but the actual displacement of the hand gradually deviated so that the path that the hand travelled was eventually rotated to a full 30° CCW from the cursor. This meant that there was no performance error signal (or no difference in actual versus expected sensory feedback), as the cursor always moved directly to the target. In this way, we could test whether just repetitively experiencing a discrepancy between vision and proprioception (what we called a cross-sensory discrepancy training signal) was sufficient to lead to changes in hand proprioception and movement, and how these changes compared with those produced following typical visuomotor adaptation (which consists of both motor performance errors and cross-sensory discrepancy errors).

We found that following exposure to the cross-sensory discrepancy between seen and felt hand motion, proprioceptive estimates of hand position were shifted in the direction of the distortion (hollow bars in Figure 5A; Cressman & Henriques, 2010), and were shifted by the same magnitude as that produced following adaptation to a visuomotor rotation of 30° CW when participants actively and voluntarily directed their visually guided reaches toward the target (Figure 5A, solid bar; Cressman & Henriques, 2009). Moreover, when we had participants reach to the same targets without visual feedback following exposure to this cross-sensory discrepancy, their reaches were also significantly deviated like the aftereffects produced following visuomotor adaptation training, although only about a third of the size (Cressman & Henriques, 2009, 2010). In fact the “aftereffects” in this study were about the same size as, and were significantly correlated with changes in proprioceptive misestimates of the hand (Figure 5B). This is in contrast to the lack of correlation between aftereffects and changes in proprioception following visuomotor adaptation (e.g., Figure 3B). Thus, these aftereffects following

mere exposure to a cross-sensory discrepancy may be due to a change in felt hand position rather than any real motor recalibration.

This in turn begs the question whether aftereffects following visuomotor adaptation are the combined result of this sensory, as well as motor, recalibration (schematic in Figure 5A, right panel). If so, then performance or movement errors are not the only training signals used for adapting reaching movements because we find open-loop reaching errors consistent with the distortion even when this error or training signal is eliminated (the cursor always moves to target so there is no discrepancy between the desired/predicted and actual movement). Instead, our results suggest an additional training signal—one based on cross-sensory discrepancy—which also independently contributes to change in movements associated with motor learning.

We can also explain our results in a slightly different manner that is consistent with the source-estimation model of Berniker and Kording (2008). According to Berniker and Kording’s model, changes in movements following motor learning can be explained by how the nervous system estimates the sources of the motor errors (e.g., whether the errors are attributed to estimated changes in limb properties versus changes in the environment). The errors or sensory discrepancy that leads to changes in felt hand position may be due an adapted representation or internal model specific to the limb, while further changes in movement (marked in purple in Figure 5A) may partly reflect adaptation to the internal representation or model of the world. Likewise, differences in sensory and motor aspects of learning may reflect specialized functions of different brain areas like the parietal cortex and cerebellum. In a recent review, Shadmehr and Krakauer (2008) proposed that a possible function of the parietal cortex is to update and integrate actual and predicted sensory feedback of the limb for state estimation, while the function of the cerebellum involves forming the internal models necessary for predicting the sensory outcome of motor commands, and correcting these motor commands through internal feedback. Consequently, the (transient) recalibration of hand proprioception could be occurring within the parietal cortex (perhaps along with premotor cortical areas), while the changes in the motor commands likely involves modifications within the cerebellum.

Further research is necessary to determine how and to what extent motor learning paradigms produce such changes and the role of sensory recalibration in motor learning. A clearer understanding of the mechanisms underlying sensorimotor learning could lead to improved rehabilitation and better motor-skill training regimes for individuals suffering from neurological disorders causing sensorimotor malfunction, as it may be possible to improve motor function by sensory adaptation. In particular, for individuals with severe motor deficits (and thus unable to complete certain motor tasks), it may be possible to alter learning conditions such that individuals are exposed to a cross-sensory discrepancy, without being required to perform the movement. Our results

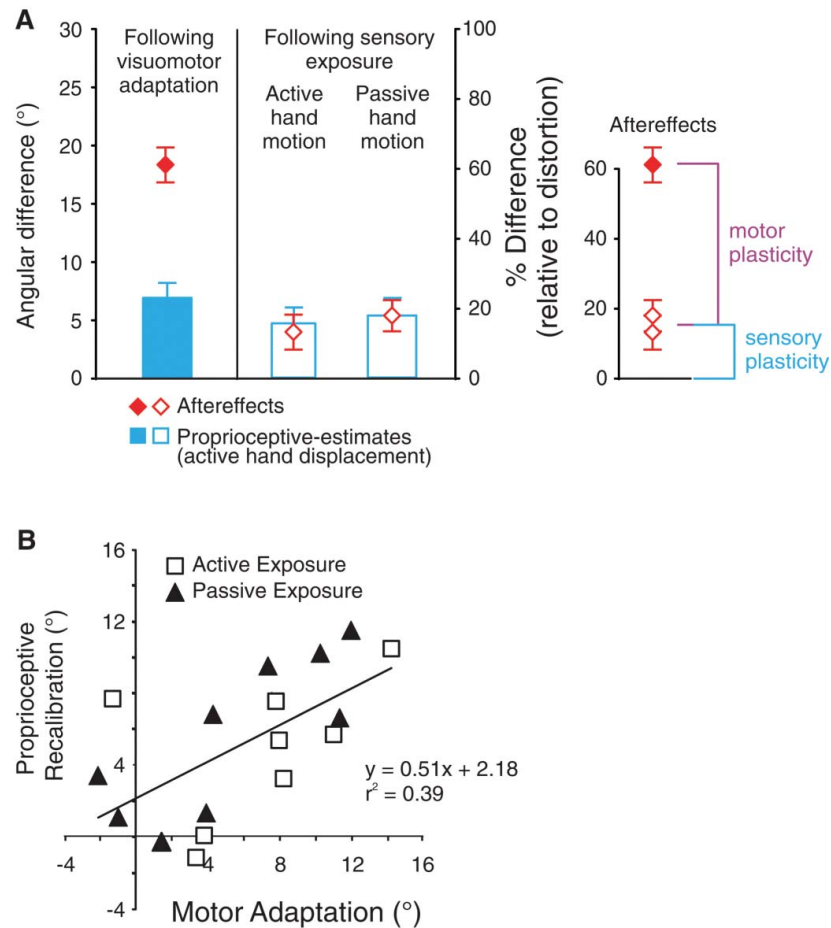


FIGURE 5. (A) Comparison between changes in proprioceptive biases and aftereffects expressed in degrees or as a percentage of the distortion introduced. In (A) we compare the changes in proprioceptive biases and aftereffects following visuomotor adaptation (leftward blue filled bar and red filled diamond, respectively) to changes arising following exposure to a cross-sensory discrepancy. Participants were exposed to the sensory discrepancy either when they were actively moving their hand outward along a constrained path (active hand motion task) or when the robot moved their hand out along the constrained path so that the cursor achieved the target (passive hand motion task). In the panel on the far right we depict the percentage of the aftereffects that could be due to sensory and motor plasticity. Error bars reflect standard error of the mean. (B) Changes in proprioceptive recalibration and motor adaptation following active (squares) or passive (triangles) exposure to the sensory discrepancy. Each symbol represents the percentage change in bias and percentage change in aftereffects averaged across reference markers and target locations for each participant. The solid line indicates the line of best fit for all data points (from Cressman & Henriques, 2009, 2010). (Color figure available online).

suggest that exposure to this error signal could then facilitate motor learning. To establish the mechanisms underlying sensorimotor learning, we are presently investigating how sensory and motor changes generalize to different areas of the workspace, as well as looking at retention of sensory and motor changes over time. By determining the relationship between sensory and motor changes, under these different task constraints we will look to determine the influence of sensory recalibration on motor learning.

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