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RESEARCH ARTICLE

The effect of visuomotor adaptation on proprioceptive localization: the contributions of perceptual and motor changes

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Abstract Reaching movements are rapidly adapted following training with rotated visual feedback of the hand (motor recalibration). Our laboratory has also found that visuomotor adaptation results in changes in estimates of felt hand position (proprioceptive recalibration) in the direction of the visuomotor distortion (Cressman and Henriques 2009, 2010; Cressman et al. 2010). In the present study, we included an additional method for measuring hand proprioception [specifically, proprioceptive-guided reaches of the unadapted (left) hand to the robot-guided adapted (right) hand-target] and compared this with our original perceptual task (estimating the felt hand position of the adapted hand relative to visual reference markers/the body midline), as well as to no-cursor reaches with the adapted hand (reaching to visual and midline-targets), to better identify whether changes in reaching following adaptation to a 50° rightward-rotated cursor reflect sensory or motor processes. Results for the proprioceptive estimation task were consistent with previous findings; subjects felt their hand to be aligned with a reference marker when it was shifted approximately 4° more in the direction of the visuomotor distortion following adaptation compared with baseline conditions. Moreover, we found similar changes in the proprioceptive-guided reaching task such that subjects misreached 5° in the direction of the cursor rotation. However, these results were true only for proprioceptive-guided reaches to the adapted hand, as reaches to the body midline were not affected by adaptation. This suggests that proprioceptive recalibration is restricted to the adapted hand and does not generalize to the rest of the body; this truly reflects a change in the sensory representation of the hand rather than changes in the motor program. This is in contrast to no-cursor reaches made with the adapted hand, which show reach after-effects for both visual targets and the midline, suggesting that reaches with the adapted hand reflect more of a change in the motor system. Our results also shed light on previous studies that may have misattributed these sensory and motor changes.

Keywords Proprioception · Reaching · Proprioceptive recalibration · Multi-sensory integration · Visuomotor adaptation

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Introduction

When making visually guided reaches, it is generally thought that vision plays a dominant role in the planning and execution of movements (Held and Bauer 1974). In situations where vision and proprioception no longer provide consistent information, the central nervous system (CNS) typically alters its motor commands in such a way that the visual representation of the hand will reach the target location. For example, when the visual location of the hand is altered and movements no longer look correct, the brain adapts its movements to this perturbation or change in the environment; this process is called visuomotor adaptation.

Whether visuomotor adaptation leads to changes in felt hand position has been recently studied following

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adaptation to a misaligned hand cursor, i.e. using virtual reality environments (Simani et al. 2007; van Beers et al. 2002). For example, Simani et al. (2007) had subjects adapt their reaches to a translated hand cursor, and, upon removal of this cursor, observed deviated movements (after-effects) to both visual and proprioceptive hand-targets, which were attributed to proprioceptive recalibration. However, subjects were asked to make goal-directed reaching movements with their adapted hand, making it difficult to determine whether the changes were exclusively due to proprioceptive recalibration. It is possible that they were due to motor recalibration as subjects made goal-directed movements.

This motor confound is particularly evident in the older literature using prisms, which again suggests that visuomotor adaptation and the presence of after-effects may be due to the recalibration of felt hand position such that subjects' felt hand position begins to match the seen (albeit distorted) image of the hand (Craske and Gregg 1966; Harris 1963, 1965; Hay and Pick 1966; Redding et al. 2005; Redding and Wallace 1988, 1996, 1997, 1978 2001, 2002, 2003, 2006; Templeton et al. 1974). These ideas are founded on results from studies that have shown comparable deviations between reaches to proprioceptive and visual targets following adaptation of reaches to visual targets with laterally displacing prisms; where proprioceptive targets can either be the perceived position of the body midline (Harris 1963, 1965; Hay and Pick 1966; Redding et al. 2005), or the felt location of the unadapted hand (Craske and Gregg 1966; Harris 1965). For example, Hay and Pick (1966) found that when blindfolded subjects pointed to a location projected from their body midline (e.g. nose), their reaches deviated by approximately 2.8° following exposure to wedge prisms (which shifted the visual field by 11°) compared with the 6° error produced when reaching to visual targets. Also, Craske and Gregg (1966) showed that following prism adaptation to visual targets, subjects' reaches deviated by approximately 4° when pointing to their unadapted hand and that these deviations were similar to those made to visual targets (again without prisms) following adaptation (which was about 1/3 of the visual distortion of 11°). Interestingly, in a recent study using a similar paradigm in which the visual field was distorted through prisms, researchers found that there were only significant after-effects when reaching to visual targets, but not when reaching to proprioceptive targets, i.e. the unadapted left index finger (Bernier et al. 2007).

From the studies discussed above, it is apparent that adapting to prisms when reaching to visual targets can sometimes lead to changes in reaches to proprioceptive targets. However, it is still unclear whether these changes in reaches to proprioceptive targets truly measure sensory recalibration. Reaching errors could be due to motor adaptation of the end-effector, or a recalibration of visual space (given that prisms displace not only ones' hand, but also the target and entire workspace). Thus, it becomes difficult to conclude how the brain is determining the source of reaching errors and distinguishing whether these errors are due to changes in proprioception, visual perception of the workspace, or the motor system (Berniker and Kording 2008; Clower and Boussaoud 2000). Therefore, it seems reasonable to conclude that visuomotor adaptation using prisms may not necessarily lead to proprioceptive recalibration.

More recent studies by Synofzik et al. (2006, 2008) and Izawa et al. (2012) have (somewhat) avoided this potential motor confound by using a different measure of perceived movement of the unseen hand. In these studies, subjects either used a mouse (moved with their left hand) or reached with their left hand to indicate the location at which their unseen adapted hand had crossed (movement trajectory) a specified border both before and after adaptation to a rotated cursor. In all three studies, training with altered visual feedback of the hand led to significant changes in the perception of this unseen and remembered hand movement direction in healthy individuals (Izawa et al. 2012; Synofzik et al. 2006, 2008). However, these studies assessed adaptation-induced changes in the perception of *remembered* movement and were not designed to measure online proprioceptive estimates of hand position. In fact, the authors interpret their results as changes in the ability of subjects to predict the sensory consequences of their movements, as opposed to proprioceptive recalibration.

Studies from Henriques et al. use methods to assess changes in felt hand position directly, which avoid goal-directed movements (and hence, the motor confound entirely), in order to determine to what extent visuomotor adaptation leads to this proprioceptive recalibration, apart from motor recalibration. To measure proprioceptive sense of hand position (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Jones et al. 2010, 2012; Salomonczyk et al. 2011, 2012), we used a robotic manipulandum to either passively place subjects' hands, or provide a guided path for subjects to actively move their hand out along to various locations in the horizontal workspace. Once the hand was placed in one of these locations, either a dot would appear or a beep would sound. Subjects would then decide whether their unseen hand was to the left or right of the body midline (signalled by a beep), or a visual reference marker (dot projected just above the plane of the hand). Because the reference marker appeared only after the hand was placed (actively or passively) in its final position, the reference marker could not be treated as a target. As well, this method does not allow the hand to freely move, thus eliminating goal-directed movements. Using subjects' responses, we were able to compute a perceptual measure of felt hand position at each reference location.

In the original study by Cressman and Henriques (2009), similar changes in felt hand position were observed regardless of whether these estimates were made when the hand was actively moved into position along a robot-generated grooved path, or when the hand was passively placed into position. Moreover, similar changes in felt hand position were observed for both the body midline and visual reference marker locations. Specifically, changes in estimates of felt hand position were shifted about 6° in the direction of the visual feedback provided following training to a 30° rightward cursor rotation, or about 0.8 cm following exposure to a 4-cm lateral cursor translation (Cressman and Henriques 2009). In both cases, a change in felt position was about 20 % of the magnitude of either cursor deviation introduced (rotated or translated). This was the case if the cursor rotation was gradually introduced, like in our original study, or was abruptly introduced, for both the left and right hands (Salomonczyk et al. 2012). This proportional change held even when we gradually increased the cursor distortion, from 30° to 50°, and then finally to 70°. Both the after-effects and change in bias similarly increased after training with each amplification of the rotation, although the extent of these relative proprioceptive and motor changes was not correlated with each other (Salomonczyk et al. 2011).

The adaptation-induced change in estimates of unseen hand position found in the Henriques laboratory is far smaller than that found in the studies by the Shadmehr, Thier and Lindner laboratories investigating how adaptation affects estimates, or predictions, of unseen hand movements. Specifically, the amount of change observed in these studies (Izawa et al. 2012; Synofzik et al. 2006, 2008) was anywhere from 1/3 to 2/3 of the visual distortion, which is much larger than the robust and consistent change of 20 % found in the perceptual tasks used in several of the Henriques papers. Although this larger change could partly be due to the fact that subjects were estimating their remembered, or what they called predictive, reaching movements, rather than a final location of the stationary hand, it is unlikely; people should be poorer at locating a remembered or predictive hand movement, compared with a stationary position of the hand where online proprioceptive signals are still available (Jones et al. 2012). Alternatively, it is possible that the reasons for larger changes in felt hand motion reported by other laboratories are due to the fact that in these studies, the hand-target was actively placed by the subject in the direction of their choosing. Thus, in these tasks, there is the possibility that adjustments of forward models add to the effect of adaptation of their sense of hand motion. Also, it is possible that the task goal could be driving these differences. There could be differences in the extent by which visuomotor adaptation affects how we localize the stationary unseen hand or the movement direction, depending on which task is used for localization such that visually induced changes may be larger when people have to reach to, rather than estimate, a hand location. The smaller change observed in the perceptual, or estimation, task is consistent with the results of Ostry et al. (2010) who found that after adapting to a force field, subjects showed a significant change in their sense of hand movement using a similar perceptual task as ours; their perceived shift in felt hand motion was about 11 % of the size of their after-effects at peak velocity. This is proportionally smaller than the shift we usually find which is about 33 % of the size of our after-effects (or 20 % of the visual distortion introduced). This then raises the possibility that task goal may influence proprioceptive localization, much like it does visual localization (Goodale and Milner 1992), perhaps by changing the value associated with proprioceptive information or the way that it is used by the CNS (Djikerman and de Haan 2007; Jones et al. 2012). In other words, the processing of proprioceptive information when it is used to guide a goal-directed movement may differ from the processing of proprioceptive information for perceiving limb position.

In order to explore how these different processes may be affected differently by visuomotor adaptation, we had subjects' complete two proprioceptive-guided tasks, specifically our proprioceptive estimation task and a proprioceptive-guided reach task similar to that used by Izawa et al. (2012). We also included another variable in this study; we asked people to reach to the midline both with the unadapted and adapted hand. This gives us the advantage of trying to make better sense of the literature discussed above in which there was a motor confound, where subjects used the adapted hand to do the reaching rather than serving as the target. In our study, by comparing no-cursor reaches with visual targets, proprioceptive hand-targets and the body midline, along with perceptual changes in felt hand position, our aim in the current study was to identify whether changes in proprioceptive-guided reaches (whether to the unseen adapted hand or midline) reflect motor changes or proprioceptive changes. In accordance with the goal of the current study, we did not use the trained hand as the reaching hand (it served as the target in many cases) in order to isolate changes in proprioception from changes in the motor computations. We hypothesized that reaches made with the unadapted left hand to the adapted right hand following visuomotor adaptation would show similar changes to those observed following the proprioceptive estimation task, in which subjects would indicate that their hand would feel similarly shifted to the right following reach adaption to a rightward-rotated cursor. However, we did not anticipate seeing this change in reaches made to the body midline, as we hypothesized that proprioceptive recalibration would be specific to the adapted hand.

Methods

Subjects

Twenty-one healthy adults and one adolescent (mean age = 21, range = 16–27, 15 females), all of whom were right handed (as reported verbally), participated in the experiment outlined below. Initially, there were twenty-six healthy subjects, but four were removed from analyses due to the fact that they were not consistent in reporting their hand position during the proprioceptive estimation task (sometimes, they judged the location of the reference marker, or body midline, relative to the hand location rather than the other way around). Another subject was removed from all analyses involving proprioceptive-guided reaching after failing to follow the task instructions in the calibration task during session one.

Subjects were either laboratory members, or were recruited through the undergraduate research participant pool at York University (and given course credit for their participation). All subjects provided informed consent, and the study was conducted in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee. All subjects had normal or corrected-to-normal vision. Because of an error in task instructions for the proprioceptive-guided reaching task (described in more detail below), 19 additional subjects (mean age = 23, range = 18–27, 9 females) were recruited through the undergraduate research participant pool at York University to repeat a subset of the experiment to correct for the instruction error.

Apparatus

A view of the experimental set-up is provided in Fig. 1a. Subjects were seated in a chair that could be adjusted with respect to height and distance from the display so that they could comfortably see and reach to each of the target locations presented on a reflective screen. With their right hand, subjects held onto the vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) such that their thumb rested on top of the handle. The reflective screen was mounted on a horizontal plane 8.5 cm above the two-joint robotic arm. Visual stimuli were projected from a monitor (Samsung 510 N, refresh rate 72 Hz) located 17 cm above the robotic arm such that images displayed on the monitor appeared to lie in the same horizontal plane as that of the robotic arm. Visual feedback of the hand's initial location during the proprioceptive-guided reaching task and visual feedback of the hand's location at all targets during calibration was provided by a white LED light mounted on the top of the robot handle, illuminating subjects' right thumb. A 43 (length) × 33 (width) × 0.30 (height) cm thick touch

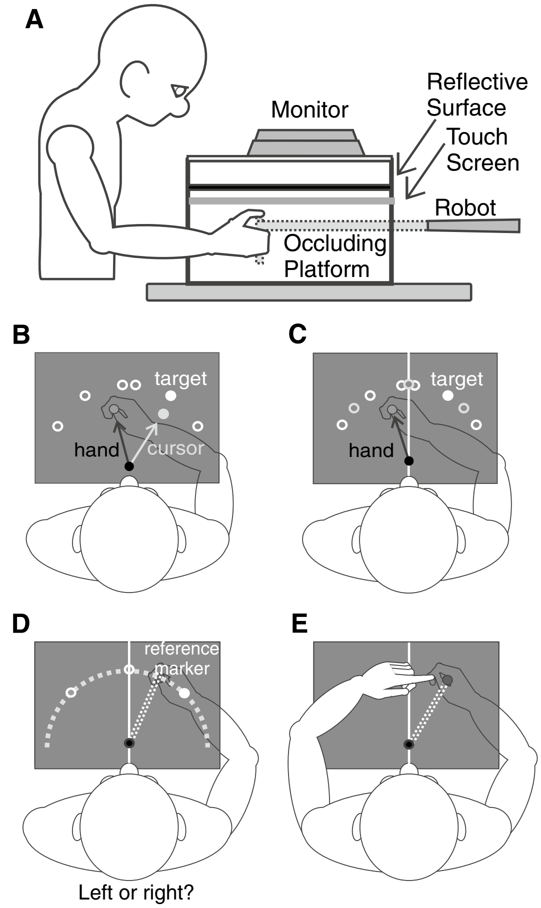

Fig. 1 **a** Side view of the general experimental setup. The reflective surface is removed when subjects need to access the horizontal touch screen panel. **b**–**e** Top views of the experimental setup. **b** *Reach training* the centre home position was represented by a 1 cm *circle* (shown in *black*), which was visible only before the trial began and was located about 20 cm in front of subjects' torso. Targets are represented by *white circles* and were located along a circular arc at a distance of 10 cm from the home position. Reach targets were located at 5°, 30°, and 60° left and right from the body midline (0°). The cursor (representing the hand) was aligned with the actual hand position during session 1 (not shown). The cursor was rotated 50° to the right with respect to the actual hand position during the rotated-reach training condition (shown in *grey*). **c** *Reaching without a cursor* trained targets are represented by *white circles* at 5°, 30°, and 60° left and right from centre. Novel targets are represented by *grey circles* at 0°, as well as at 45° left and right from centre. Additionally, there was a novel proprioceptive body-midline target (shown by *white line*). All targets were located at a distance of 10 cm from the home position. **d** *Proprioceptive estimation* for this task, subjects actively moved their hand along a robot-generated groove (shown by the *white rectangle*) to a location at the end of the *grey dotted arc*. Once the hand had arrived at this location, a reference marker appeared: either a visual dot (*white circles*) or a beep to signify the body-midline reference marker (*white line*). Visual references were located at 0°, as well as 45° left and right from centre and were 10 cm from the home position. **e** *Proprioceptive-guided reaching* subjects made proprioceptive-guided reaches with their left hand to the felt location of their right hand (locations not shown), and this hand-target was guided to these locations by moving out along a robot-generated groove (shown by the *white dashed rectangle*). Proprioceptive targets were located at 0° and 30°, 45°, 60° left and right, as well as the body midline

screen panel (Keytec Inc., Garland, TX, USA), with a resolution of 4,096 × 4,096 pixels was horizontally mounted 5 cm above the robotic arm to record reach endpoints (made with the left hand) to proprioceptive hand-targets (the felt location of the right thumb resting on top of the robot handle). The lights were dimmed, the subject's view of their own hand was blocked by the reflective surface and a black cloth was draped over their shoulders to conceal the experimental setup. The view of the left reaching hand was not concealed and thus visible during the proprioceptive-guided reach task so that any errors when reaching to the midline, or the unseen right-target hand, could not be attributed to errors in localizing the reaching hand.

Procedure

All tasks were completed in two test sessions (within a 2 week period), which explored the influence of different visual feedback conditions on proprioceptive recalibration (changes in felt hand position). Each testing session consisted of five distinct tasks, although nine tasks were completed in each session as some tasks were repeated (See Fig. 2). The first session had subjects reach to visual and proprioceptive targets after training (Task I) to reach with a cursor which was *aligned* with their hand's position (Fig. 2; box 1). The second session, however, had subjects complete the same trials after training with a cursor which was *misaligned* from their hand's position (Fig. 2; box 1). The misaligned cursor was rotated 50° rightward from their actual hand position, with this rotation being introduced gradually by 0.75° per trial. In both sessions, subjects completed two blocks of proprioceptive-guided reaches (Task III; pointing with the left index finger on a horizontal touch screen panel to the felt location of their right thumb underneath). Additionally, subjects completed a proprioceptive estimation task (Task IV) in which they reported the felt location of their right hand in reference to visual reference markers and the body midline. Finally, subjects completed reaches without a cursor (Task II) at four different times on each testing day, once after each of the reaching, proprioceptive-guided reaching and proprioceptive estimation tasks. The additional subjects we recruited only completed the first five tasks in each session (Fig. 2; boxes 1–7), as well as the final proprioceptive-guided reaching calibration task (Fig. 2; box 12).

Task I: visually guided reach training

Subjects held onto the robotic manipulandum with their right hand and were instructed to reach to one of the six reach targets as quickly and as accurately as possible, with either an aligned (session 1) or rotated (session 2) cursor representing their hand's position (Fig. 1b). During training there were 6 reach targets, represented by 1 cm diameter yellow circles (white circles in Fig. 1b). The reach targets were located radially, 10 cm from the home position at 5, 30 and 60°, both left and right of centre (body midline). During both sessions, the cursor was a green circle 1 cm in diameter. The home position, which was not visible in this task, was located 20 cm in front of the subjects, along their body midline. After placing the hand at the home position for 300 ms, 1 of the 6 reach targets would appear. Visual feedback of the hand's position became available only when subjects had travelled 4 cm away from the home position. Subjects were required to attain the target and could correct their movements as much as they desired before a reach trial was considered complete. A reach trial was complete when the centre of the hand cursor intersected the target (i.e. was within 0.5 cm of the target's centre). After the reach was complete, both the cursor and target vanished and the subject moved their hand back towards the non-visual home position, guided by the robot which constrained the movement along a grooved path that ended at the home position. If subjects tried to move outside of the path, a resistance force [proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s)] was generated perpendicular to the grooved path (Henriques and Soechting 2003). The six reach targets were presented pseudo-randomly such that each target was presented once before any target from the set was repeated. Each subject completed 126 reach trials in the aligned session and 200 in the misaligned session.

Task II: reaching without a cursor

One of the traditional methods of assessing reach adaptation is to look at changes in reaches made without any visual feedback before and after training with a misaligned cursor. These changes are known as after-effects. Thus, after training (Task I) in each session, subjects performed 20 more reaches without the cursor to the same six targets as in training (white circles in Fig. 1c), as well as four additional ones, including the body midline (white line in Fig. 1c), and three other visual targets (0°, and 45° left and right of centre; grey circles in Fig. 1c), for a total of 10 reach targets. "Midline reaches" were cued by a beep. After the hand had moved out towards the target and been held in the same position for 500 ms the target disappeared indicating that trial was over. Subjects returned their hand back to the home position by following the grooved path.

Task III: visually guided reaching and proprioceptive-guided reaching

This task began with five visually guided reaches using either an aligned (session 1) or rotated (session 2) cursor to

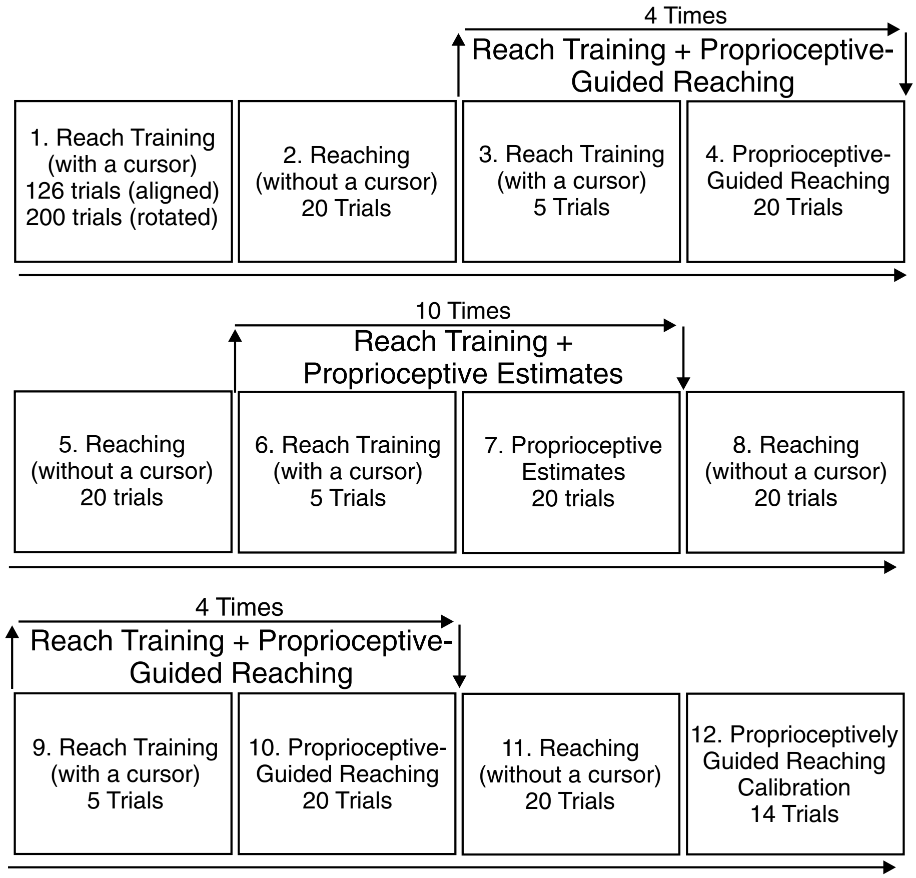

Fig. 2 A breakdown of the experiment tasks within each session. Subjects began the session by reaching to visual targets while a cursor accurately, or inaccurately (rotated 50° rightward with respect to the actual hand location) represented the location of their right hand (*box 1*). After completing 126 visually guided reach trials (or 200 in the misaligned condition), subjects reached to each of the ten reach targets (six trained and four novel targets) twice without the cursor, to assess visuomotor adaptation (reach after-effect trials, *box 2*). This was followed by four sets of five visually guided reaches (*box 3*) and 20 proprioceptive-guided reaches (*box 4*) with the left hand, to the unseen right/adapted hand. Subjects then completed another block of after-effect trials (*box 5*). This was followed by ten sets of five visually guided reaches (*box 6*) and 20 proprioceptive estimates (*box 7*). This was again followed by another block of after-effect trials (*box 8*). Then subjects completed another four sets of five visually guided reaches (*box 9*) and 20 proprioceptive-guided reaches (*block 10*), followed by yet another block of after-effect trials (*box 11*). Once all experimental tasks were completed, subjects did 18 calibration trials (*box 12*) for the proprioceptive-guided reaching task

six targets much like in the reach training trials. The rest of the trials in this task involved proprioceptive-guided reaching (Fig. 1e), and for this purpose the reflective screen was removed from the shelving unit by the experimenter so that subjects had access to the touch screen panel.

In this task, proprioceptive hand-targets included the felt location of the right thumb (resting on the top of the modified handle of the robot) when it was 10 cm from the home position, along a radial arc at the locations of 0° and 5°, 30°, 45°, and 60° left and right relative to 0° (not shown). Proprioceptive hand-targets (the right thumb) were made visible by an LED light on the robot hand when at the home position, and were continuously visible for the calibration trials at the end of the experiment. The 8th proprioceptive-guided reaching target was a location along the body midline (white line in Fig. 1e).

Subjects initiated a trial with their right hand holding the robot handle at the home position, which was made visible by a white LED light mounted on top of the handle. Subjects were instructed to reach out with their visible left hand and, using their left index finger, touch the horizontal touch screen panel at the *seen* location of their right thumb at the home position (black circle in Fig. 1e). The light then turned off and the subject moved their right hand along a 10 cm robot-generated grooved path from the home position (white dashed rectangle in Fig. 1e), to 1 of the 7 proprioceptive (adapted hand) target locations. Thus, the robot specified the direction and final location of this adapted hand. Subjects then reached out with the left unadapted hand (from the home position), and used their index finger to touch the surface (on the touch screen panel) just above the *felt* location of their right thumb. The adapted right hand then followed a robot-generated groove back to the home position, and the LED light was illuminated again to start the next trial. For trials in which the body midline was cued, subjects would again start with both hands at the home position. After the light indicating the seen location of the right thumb turned off, they were instructed to reach forward with the left hand to a position along the body midline. Subjects made 20 reaches to the 8 proprioceptive targets (either the unseen right hand or body-midline target) before the reflective screen was put back into position, so subjects could make 5 visually guided reaches (training purposes). This procedure repeated itself 4 times until a total of 100 trials had been completed (20 visually guided reaches and 80 proprioceptive-guided reaches, 10 to each hand-target or body midline).

Task IV: visually guided reaching and proprioceptive estimates

To assess proprioceptive acuity and sensitivity, we used a similar proprioceptive estimation task as in previous studies from our laboratory (Fig. 1d). The purpose of the proprioceptive estimation trials was to determine the position at which subjects perceived their unseen hand was aligned with each of the reference markers (as a measure of accuracy), as well as the uncertainty ranges (precision) associated with these estimates. These estimation trials were interleaved with reach training trials completed after training with an aligned cursor (session 1) and with a misaligned cursor (session 2) so that we could assess baseline proprioceptive sensitivity of hand position (in session 1), in addition to whether these estimates of felt hand position change with visuomotor adaptation of the hand movements (in session 2). Reach trials and proprioceptive estimate trials were systematically interleaved during this task to ensure that adaptation was maintained.

The proprioceptive estimation task had three visual reference markers, represented by 1 cm diameter yellow circles, as well as a proprioceptive reference marker (the body midline, represented by a white line in Fig. 1d). Reference markers for the proprioceptive estimation task were located radially, along an arc 10 cm from the home position, at 45° both left and right of centre, as well as at centre (0°) (Fig. 1d). The centre reference marker was either a visual reference marker or the body midline.

Subjects began by reaching 5 times to the same visual reach targets as in the training trials with either an aligned cursor (session 1) or rotated cursor (session 2). The reaches were immediately followed by 20 proprioceptive estimates, in which subjects were instructed to push their right hand out along a linear robot-generated path (this was done actively, to reduce the duration of the experiment) until the path ended at a particular location (white line in Fig. 1d). Once the hand arrived at this location, a reference marker appeared; which could either be a dot (white circles in Fig. 1d) or a beep to indicate the body midline (white line). Subjects then pressed a left or right key (arrow keys on a standard keyboard, located comfortably to the left of their body) with their left hand to indicate whether their right hand felt left or right of the reference marker, respectively. The position of the hand relative to each marker (and thus, the direction of the robot-generated groove) was determined using an adaptive staircase algorithm (Kesten 1958; Treutwein 1995). Each of the four reference markers had 2 staircases: one starting 20° left of the reference marker and another 20° right (See Cressman and Henriques 2009, 2010). The two staircases were randomly interleaved and adjusted independently as stipulated by Cressman and Henriques (2009, 2010). This procedure repeated itself 10 times until a total of 250 trials had been completed (50 reach trials and 200 proprioceptive estimates).

Task V: proprioceptive-guided reaching calibration

The purpose of this last task was to provide a baseline measure for the proprioceptive-guided reaches to the unseen target hand in the proprioceptive-guided reaching task. Like the regular proprioceptive-guided reaching trials in the proprioceptive-guided reaching task, the reflective screen was removed so that the touch screen panel was accessible. This task was similar to the proprioceptive-guided reaching task, except the hand-target remained lit (and thus visible) at the target locations during reaches with the left hand so that these reaches could be as accurate as possible. This process was repeated until reaches to each of seven distinct target locations were made twice.

Data analysis

The goal of this study was to examine the effect of visuomotor adaption (i.e. training to reach with altered visual feedback of the hand) on hand proprioception. Changes in sense of felt hand position (or proprioceptive recalibration) were measured using both proprioceptive-guided reaches made with the unadapted hand to the adapted hand as well as with proprioceptive estimates of hand position relative to a reference marker. However, before exploring proprioceptive recalibration, we wanted to confirm that all subjects had adapted to the visuomotor distortion. We analysed reaching errors (after-effects) when reaching without a cursor to explore whether subjects adapted their reaches to the reach targets after training with a misaligned cursor and to confirm that reach adaptation was maintained throughout all tasks of the experiment. For this purpose, we analysed angular errors at reach endpoint in a two visual feedback during reach training (aligned vs. misaligned training) $\times$ 8 target repeated measures analysis of variance (RM-ANOVA).

For information on how we determined the locations at which subjects felt their hand was aligned with the reference markers in the proprioceptive estimation task (bias and uncertainty ranges), please see Cressman and Henriques (2009). A bias is a point-of-subjective-equivalence (50 % chance of responding left), and is where the hand needs to be so that it is felt to be at a position equivalent to the reference marker location. Uncertainty range is the difference between the values at which the response probability was 25 and 75 %. Following visuomotor adaptation to a rightward-rotated cursor, if the hand were to be placed on the reference marker, then they would misperceive the hand to feel more right than it was. To determine if proprioceptive recalibration had occurred in this proprioceptive estimation task, we compared biases and uncertainty ranges using a two visual feedback during reach training (aligned vs. misaligned cursor) × 4 reference marker RM-ANOVA.

We then determined whether reach training with altered visual feedback also led to changes in proprioceptive-guided reaches made with the unadapted hand to the adapted hand (as the target) and to a location along the body's midline. We measured changes in proprioceptive localization in this task by comparing the reach endpoints of the left hand to these targets following training with the rotated cursor (session 2) with those following training with the aligned cursor (session 1). We used a two visual feedback during reach training (aligned vs. misaligned cursor) × 7 target RM-ANOVA to confirm that recalibration had occurred. Due to an error in instructions for this task, most subjects from our original sample made reaches to their midline that were close to the home position, making it difficult to compare this midline target with the other hand-targets. Thus, data from the 19 additional subjects were analysed using a two visual feedback during reach training (aligned vs. misaligned cursor) × 2 target (midline vs. adapted hand at the centre target location) RM-ANOVA to determine if recalibration had occurred in this new subject group at both central targets.

We then compared changes in proprioceptive-guided reaches to changes in proprioceptive biases. Only proprioceptive-guided reaches made to targets that were in common locations as reference markers were included in the analysis (i.e. 45° left and right, and 0°). The midline proprioceptive-guided reach target was excluded from this analysis because of the problems discussed above. We used a two visual feedback during reach training (aligned vs. misaligned cursor) × 2 task (change in bias vs. change in reach endpoint errors) × 3 marker/target location RM-ANOVA.

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

Finally, we wanted to compare sensory changes in the proprioceptive-guided reaching task, changes in the proprioceptive estimation tasks, and motor changes in the no-cursor reaching tasks to see if they were related. Specifically, we compared (1) changes in after-effects with changes in proprioceptive estimates, (2) changes in proprioceptive-guided reaches to changes in proprioceptive estimates, and (3) changes in proprioceptive-guided reaches to changes in after-effects through regression analyses. Given that our new set of controls did not complete the proprioceptive estimation tasks, their midline results were not included in these comparisons.

Results

Visuomotor adaptation

We first determined the extent to which subjects adapted their reaches (i.e. the magnitude of visuomotor adaption). Reaching endpoint errors for trials made to novel targets without a cursor following reach training averaged across all subjects are displayed in Fig. 3a. Here we see that reaches following misaligned training (triangles) are to the left of those reaches following aligned training (diamonds). On average these angular changes in endpoint errors to visual targets (Fig. 3e, left grey bar, averaged across subjects, blocks, and targets) after training with a rotated cursor, compared with those made with an aligned cursor, were 12.64° more left of the target. This suggests that subjects adapted their reaches in response to training with the rotated cursor [$F(1, 21) = 96.01$, $P < 0.001$]. Furthermore, the size of reach after-effects did not diminish between reaches completed after the reach training task compared with reaches completed after the proprioceptive estimation task or proprioceptive-guided reaching tasks [$F(1.57, 32.90) = 1.90$, $P = 0.17$]. This suggests that the level of adaptation was maintained across the tasks within a testing session. Finally, changes in reach errors generalized across the workspace and these after-effects observed following training to a rotated cursor were similar in magnitude across both trained and novel targets [$F(2.77, 58.24) = 1.13$, $P = 0.34$]. More importantly, angular changes in endpoint errors to the body midline (Fig. 3e, left white bar) were similar to changes observed at visual targets. Overall these results suggest that subjects adapted their reaches to all targets after training to reach with a rotated cursor.

Proprioceptive estimates—bias and uncertainty range

In Fig. 3b we show the positions at which subjects perceived their hand was aligned with the reference markers (circles) after training with both an aligned (diamonds) and

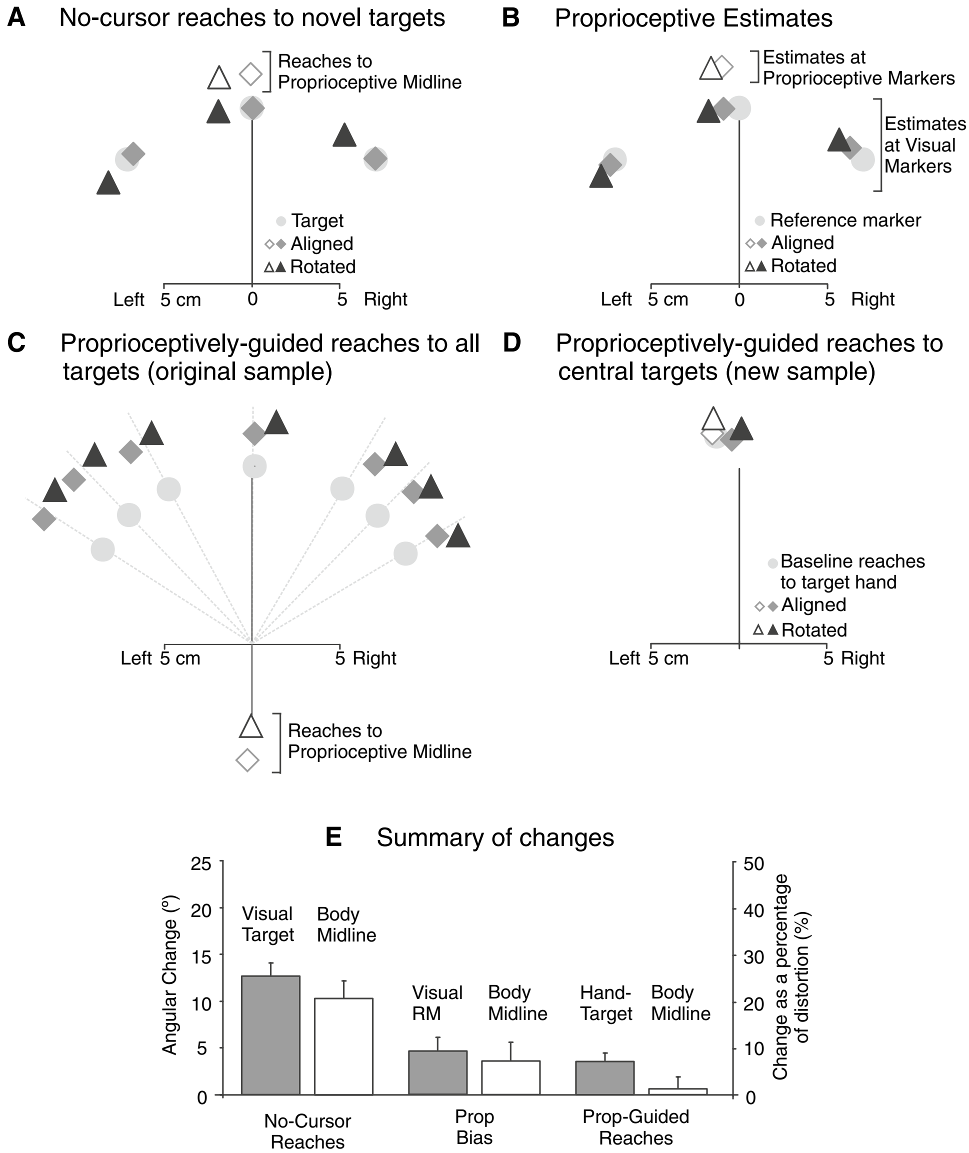

Fig. 3 **a** Mean 2-D no-cursor reaches, after subjects trained with an aligned (*diamonds*) or rotated (*triangles*) cursor. Reaches to visual targets (*circles*) are represented by *shaded symbols*. Reaches to the body midline (or proprioceptive target) are represented by *white filled symbols*. **b** Mean 2-D estimates of felt hand position after subjects trained with an aligned (*diamonds*) or rotated (*triangles*) cursor. Estimates with respect to visual reference markers (*circles*) are represented by *shaded symbols*. The proprioceptive estimates relative to the body midline (or proprioceptive marker) are represented by *white filled symbols*. **c** Mean 2-D proprioceptive-guided reaches after the original group of subjects trained with an aligned (*diamonds*) or rotated (*triangles*) cursor. Proprioceptive-guided reaches with respect to hand-targets (*circles*) are represented by *shaded symbols*. The proprioceptive-guided reaches to the body midline (or proprioceptive target) are represented by *white filled symbols*. **d** Mean 2-D proprioceptive-guided reaches in the new subject group to central targets only. **e** Summary of changes in angular error at reach endpoints in the no-cursor reaches (*left: shaded bar* for visual target, *white bar* for midline target), proprioceptive biases (*middle: shaded bar* for visual markers, *white bar* for midline marker) and proprioceptive-guided reaching (*right: shaded bar* for hand-target, *white bar* for midline target) tasks after training to reach with a rotated cursor. Changes are shown for all tasks in degrees and as a percentage of the distortion. *Error bars* reflect standard error of the mean

rotated (triangles) cursor. Specifically, we can see that subjects' estimates of their unseen hand positions were slightly biased (on average 4.77°) to the left of each marker after training with an aligned cursor (diamonds). Here, a leftward bias indicates that the hand feels shifted to the right (see "Methods" section for explanation). However, after visuomotor adaptation, proprioceptive estimates of hand position were shifted significantly leftward of the aligned estimates (diamonds) [$F(1, 21) = 10.57$, $P < 0.01$]. On average, estimates after training with a rotated cursor were 9.16° left of the reference markers. Furthermore, these changes in estimates of hand position were observed at all reference markers [$F(2.38, 49.95) < 1$], regardless of whether the centre reference marker was the body midline or a visual reference [$F(1, 21) < 1$]. Estimates at visual markers were 4.65° more left than after training with an aligned cursor (middle grey bar in Fig. 3e) while estimates at the body midline (middle white bar) were 3.61° more left after training.

As in other studies from our laboratory visual feedback during the training trials had no influence on subjects' uncertainty ranges [$F(1,21) < 1$], regardless of the reference marker location [$F(3,63) = 1.08$, $P = 0.19$].

Proprioceptive-guided reaching

Finally, we wanted to determine if adapting reaches to a visually rotated hand cursor also leads to changes in proprioceptive-guided reaches. Figure 3c shows these reaches to proprioceptive hand-targets (circles), averaged across subjects after training to reach with both an aligned (diamonds) and rotated (triangles) cursor. The original midline data is plotted in Fig. 3c, but was excluded from statistical analysis because many of these reaches were close to the home position. We see that in the aligned session subjects did overshoot the target, but that the mean angular error was only 0.82° (when the midline data was excluded) from the target. However, more importantly, after training to reach with the rotated cursor, proprioceptive-guided reaches were shifted significantly to the right of the reaches made after training with the aligned cursor except for the centre midline location that was omitted from the analysis (but shown in 3D) [$F(1, 20) = 34.00$, $P < 0.01$]. This significant shift, however, did not further vary across target locations [$F(1.96, 39.24) = 1.83$, $P = 0.17$]. On average, the angular error after training with a rotated cursor was 5.93° right of the target (when the midline data was excluded), and 5.10° more right than after training with an aligned cursor.

We also wanted to determine if these changes in proprioceptive-guided reaches generalized to the body midline. These midline reaches from the original sample of subjects are represented in Fig. 3c by hollow symbols. We can see that, although most of these reaches were close to the home position, after training to reach with a misaligned cursor they do not appear to have as much of a rightward shift as those found at the hand-targets. However, given that they were so close to the home position we could not compare these midline reaches to those to the adapted hand in our original sample. Figure 3d shows these reaches (to the midline and centre hand-target only) with a new sample of subjects, averaged across subjects after training to reach with both an aligned (diamonds) and rotated (triangles) cursor. We found that, although reaches to the adapted hand (solid symbols) shifted significantly rightward following adaptation, those to the midline (hollow symbols in Fig. 3d; right white bar in Fig. 3e) did not. This confirms the original finding that this effect does not generalize to the body midline [$F(1,18) = 4.58$, $P = 0.05$].

The changes in proprioceptive-guided reaches to hand-targets were similar to the changes observed in subjects' biases (Fig. 3e, right grey bar). Specifically, there was no difference between the magnitude of proprioceptive recalibration and the change in proprioceptive-guided reaching for the 3 locations (45° left and right, and 0°) that both tasks had in common [$F(1.87, 37.45) = 0.34$, $P = 0.70$]. However, if we plot these changes in proprioceptive-guided reaches (as a percentage of the 50° distortion introduced, collapsed across the three targets, midline target excluded) as a function of changes in proprioceptive estimates (as a percentage of the 50° distortion introduced), we do not find a significant correlation, suggesting the processes that contribute to changes in proprioceptive localization may not be related (Fig. 4a, $P = 0.17$). Furthermore, if we plot these changes in proprioceptive-guided reaches (as a percent of the distortion introduced) as a function of reach adaptation (as a percent of the distortion introduced), again we do not find a significant correlation, which also suggests these processes may not be related (Fig. 4b, $P = 0.98$). However, when we plot changes in proprioceptive estimates (as a percent of the distortion introduced) as a function of reach adaptation (as a percent of the distortion introduced), we do find a significant correlation, which suggests that these two processes could be related (Fig. 4c, $P = 0.02$).

Discussion

The goals of the present study were to compare the perceptual and motor changes following visuomotor adaptation and to determine whether the proprioceptive recalibration typically observed following visuomotor adaptation is restricted to the adapted hand, or if it generalizes to the body midline. We had subjects adapt their reaches to a rotated hand cursor, and then determined the locations at which they felt their hand was aligned with a reference marker before and after adaptation in our proprioceptive estimation task. We compared these changes in estimates of hand position to another proprioceptive task in which subjects made proprioceptive-guided reaches with the unadapted left hand to the adapted right hand before and after adaptation. We found that following reach training with a rotated cursor subjects reached 12.40° more leftward of the target (i.e. showed after-effects). In the proprioceptive estimation task, they also recalibrated their sense of felt hand position 4.39° in the direction of the rotated cursor. Furthermore, subjects indicated, by reaching with the unadapted left hand that their unseen adapted right hand was shifted to the right 5.1° following adaptation. This last effect,

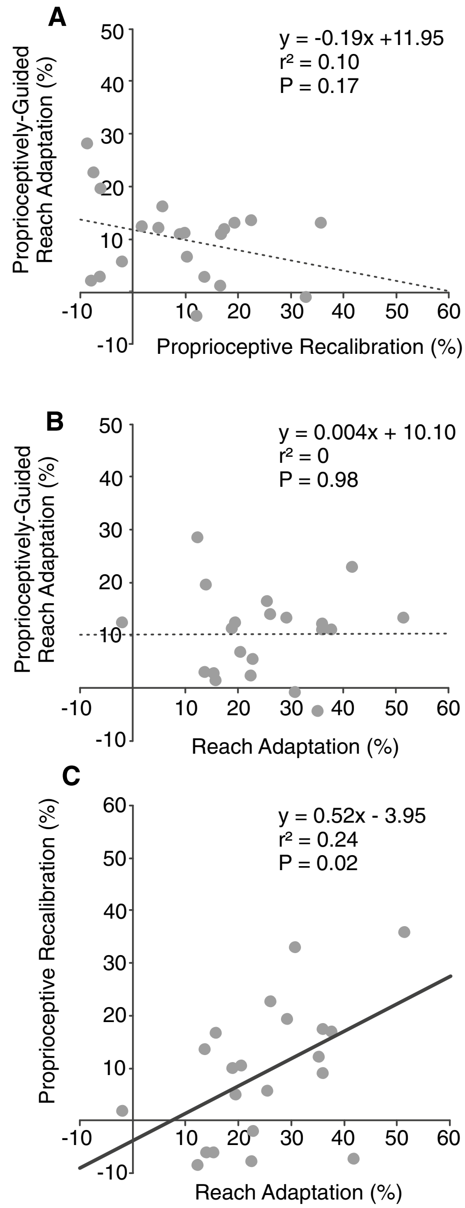

Fig. 4 **a** The changes in proprioceptive-guided reaching (as a percentage of the distortion) are plotted as a function of changes in proprioceptive estimates of hand position (as a percentage of the distortion) for each subject after exposure to a misaligned cursor compared with an aligned cursor. **b** The changes in proprioceptive-guided reaching (as a percentage of the distortion) are plotted as a function of reach adaptation (as a percentage of the distortion) for each subject after exposure to a misaligned cursor compared with an aligned cursor. **c** The changes in proprioceptive estimates of hand position (as a percentage of the distortion) are plotted as a function of changes in reach adaptation (as a percentage of the distortion) for each subject after exposure to a misaligned cursor compared with an aligned cursor

however, did not generalize to the body midline such that reaches with the unadapted hand to the body midline were similar regardless of whether subjects trained with aligned or misaligned visual feedback of the hand. In contrast, when subjects reached with their unseen adapted hand to the body-midline site, they did produce after-effects similar to those for visual targets. This suggests the latter reflects mainly a motor change rather than a sensory change. Despite a similar magnitude in proprioceptive recalibration, changes in hand localization (proprioceptive-guided reaching) and changes in estimates of felt hand position (proprioceptive estimates) were not related. Overall, these results suggest that visuomotor adaptation leads to changes in felt hand position, but that these changes do not generalize to the body midline.

Visuomotor adaptation

The proportional change in reach after-effects was ~25 % of the 50° rightward distortion introduced (Fig. 3e, left bar), and these after-effects were similar when reaching to visual targets and to a non-visual target, specifically the body midline. This magnitude of reach adaptation observed in the current study is smaller than typically found in other studies from our laboratory (Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012), and thus, like our smaller changes in proprioceptive estimates of hand position (discussed below), may have been due to some subjects not performing or learning to the same extent as subjects from previous studies. Nonetheless, the majority of our subjects did show both significant and clear changes in both reaches (after-effects) and proprioceptive estimates. In fact, only one subject failed to show any after-effects (see abscissa in Fig. 4b), and several only showed small after-effects (between 10 and 20 % of the distortion).

Proprioceptive recalibration

In the current study, the proportional change in felt hand position was ~9 % of the distortion introduced (Fig. 3e, middle bar), when estimating the unseen hand relative to both visual and proprioceptive markers, which is not surprising given that the adapted right hand was used as a reference. Like our after-effects, the magnitude of proprioceptive recalibration found in the current study is smaller than typically found in other studies from our laboratory (~25 % of the distortion) (Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012). Again, this smaller change in felt hand position is partly due to the fact that in this study, we had around 6 of our 21 subjects who changed their felt hand position in the opposite direction, and several more whose recalibration was less than 10 % in the direction of the distortion. In our other studies mentioned above, we rarely had more than one participant who failed to show a change in felt hand position. Nonetheless, these subjects who failed to show a positive change in their estimate of hand position did show positive changes in their reaches to the felt position of their hand (in the proprioceptive-guided reach task). Overall, only two subjects produced a negative change in proprioceptive-guided reaches but these two showed over 10 and 30 % proportional changes in estimates. Again, this suggests that perceptual reports and reaches to the felt hand position are not necessary related. However, it could be that there is noise in the output, when making a perceptual judgment rather than when moving to a target, that is masking a possible relationship. Even though we found that subjects adapted their visually guided reaches and recalibrated hand proprioception to a lesser extent in the current study compared with previous results, the relative proportion of proprioceptive recalibration to motor adaptation was similar (around 36 %).

Perceptual versus motor change

As mentioned above, we found comparable changes in people's sense of the position of their adapted hand, both when subjects perceptually estimated the hand's position relative to a marker and when they reached to their unseen adapted hand. While the change in perceived hand position occurred when the reference marker was the body midline, reaching to the body midline with the un-adapted hand did not produce a similar shift (in the Proprioceptive-guided reach task). This is not surprising, however, as we hypothesized that this change in proprioception is isolated to the adapted hand and thus reaches to the midline should not have shown this change. In this case, estimating the adapted hand should (and did) show a change (in the proprioceptive estimation task), independent of the sensory modality of the reference marker; but reaching to anything other that the adapted hand in the proprioceptive-guided reach task, like the midline, should not and (did not) show a change. Lastly, we did find significant after-effects in our no-cursor reaching task, where subjects were reaching to both visual targets and the body midline with their adapted hand. The combined results of these three tasks, which each use the body midline for different purposes (reference marker vs. target) and have used the adapted hand as either the target or as the end-effector, suggest that some of the observed changes are actually due to changes in the motor commands for the trained location (like the changes seen in the no-cursor reach task) while others reflect changes in felt hand position (like in the proprioceptive-guided reaching and the proprioceptive estimate task). In other words, in accordance with our hypothesis, we expected to find changes either when it is the adapted hand that was making the movement (because of motor changes following adaptation), or when it is the location of the adapted hand being assessed (here the shift can be attributed to proprioceptive changes since there is limited movement of the adapted hand along a restricted pathway). This is a useful distinction given that some earlier studies, which suggested that proprioception was recalibrated following visuomotor adaptation, may not be actually reflecting sensory changes but merely changes in motor output. That is, previous studies which assess proposed changes in proprioception, by having the subjects move their adapted hand (to either a midline or their opposite hand), could be assessing changes in the motor command following adaptation as opposed to proprioceptive recalibration (Craske and Gregg 1966; Hay and Pick 1966; Simani et al. 2007; Van Beers et al. 2002).

Now that we have shown that felt hand position changes following visuomotor adaptation, (both when the adapted hand is localized through a perceptual task or a motor task), next we look to compare our results with those showing similar results using a shifted view of the hand (either virtually or with prisms). Prism studies have investigated proprioceptive recalibration by having subjects point to proprioceptive targets following adaptation to laterally displacing prisms. To date the results have been inconsistent as one study found that subjects showed errors of about 4°, or 36 % of the distortion, when pointing with their seen adapted hand to either visual targets or the unadapted hand following prism adaptation (Craske and Gregg 1966). Another study using a similar paradigm only found changes in reach errors made with the adapted hand towards visual targets and none at proprioceptive targets (Bernier et al. 2007). Moreover, another prism study found that subjects showed errors of about 6°, or 54 % of the distortion, when pointing with their seen adapted hand to visual targets, however, reaches only deviated by about 3°, or about 25 % of the distortion, when pointing to a location projected from their body midline while blindfolded (Hay and Pick 1966). Our comparable task (no-cursor reaches) differs slightly from Hay and Pick, in that our reaches made with the adapted hand showed a similar shift both when the target was visual and when it was the body midline. In our study, the after-effects were slightly, although not significantly, smaller when reaching to the midline than when reaching to the visual target without a cursor. This could be partly due to the type of distortion (prisms displace the entire visual field, while the rotated cursor only misaligned visual feedback of the hand). Nonetheless, in all three studies mentioned, it was the adapted hand that is making the movement, and as we argued above, the changes in one's reaches could be entirely due to a resulting motor change rather than a sensory change. While this does not explain the inconsistent results discussed above between studies, we suggest that their findings may have to do with how this motor change following prism adaptation generalizes to different sensory targets (either to hand-targets or midline-targets).

More recent studies exploring proprioceptive recalibration have utilized virtual reality environments to restrict distorted visual feedback to the hand (i.e. show a cursor representing the hand's position) and these studies have tested after-effects to non-visual targets (Simani et al. 2007; Van Beers et al. 2002). Again, the distortion in these two studies differs from ours in that they use a translated shift in the visual feedback of the hand. More importantly, their results are based on moving the adapted hand to the visual or non-visual (opposite hand) targets and, while these studies find differences in the magnitude of changes that occur when reaching to a visual target compared with a proprioceptive target (although they did find a change in each case), these changes may more likely reflect motor changes that vary with the modality of the target.

Conclusion

In conclusion, we found that our proprioceptive-guided reaching task produces comparable results with our proprioceptive estimation task with respect to determining proprioceptive recalibration. Yet given that we did not see a similar shift for proprioceptive-guided reaches to the body midline, we can conclude that proprioceptive recalibration following visuomotor adaptation may be restricted to the adapted hand and not the rest of the body. Given that changes in proprioceptive estimates and proprioceptive-guided reaching were not correlated, these tasks may be assessing different processes. The combined results from our three tasks, which utilize the body midline for different purposes, suggest that some of the changes observed are due to changes in the motor commands, while others reflect sensory changes in felt hand position.

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