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RESEARCH ARTICLE

Proprioceptive localization of the left and right hands

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Abstract The present study examined the accuracy of proprioceptive localization of the hand using two paradigms. In our proprioceptive estimation paradigm, participants judged the position of a target hand relative to visual references, or their body's midline. Placement of the target hand was active (participants pushed a robot manipulandum along a constrained path) or passive (the robot manipulandum positioned participants' target hand). In our proprioceptive-guided reaching paradigm, participants reached to the unseen location of a hand; both the left and right hands served as the target hand and the reaching hand. In both paradigms, subjects were relatively good at estimating the location of each hand (i.e. relative to a reference marker or using a reach), with directional errors falling within 2 cm of the actual target location, and little variation across the workspace. In our proprioceptive estimation paradigm, biases when the target hand was passively placed were no larger than those made when the target hand was actively placed. Participants perceived their left hand to be more to the left than it actually was, and their right hand to be more rightward than it actually was, but with a similar error magnitude across target hands. In our reaching paradigm, participants' estimates of left hand location were deviated more leftwards than their estimates of right hand location, but showed a small but similar pattern of location-dependent reach errors across the two hands. Precision of estimates did not differ between the two hands or vary with target location for either paradigm.

Keywords Reach · Relative judgment · Left hand · Right hand · Active · Passive

Introduction

Our central nervous system (CNS) uses visual and proprioceptive information about the locations of our body parts to enable us to move throughout the environment and complete our daily activities. Although research has shown that we do rely heavily on vision for this localization, humans are capable of localizing a body part with minimal error in the absence of visual information. In fact, in several cases a *proprioceptive target* (i.e. a body part) may be localized more accurately than a visual target. For example, Lovelace (1989) found that when using the tip of a pen to reach to a target's location, participants were more accurate when reaching to proprioceptive targets (mean error 1.77 cm) than when reaching to visual targets (mean error 2.89 cm). Similarly, when Sarlegna and Sainburg (2007) asked participants to make right handed reaches to the unseen location of their left index finger, they found relatively small reach errors, with an average overestimation of 1.5 cm. This error was significantly smaller than when participants reached to visual targets under the same conditions, with a mean overestimation of 4.0 cm.

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One of the primary methods used to examine human accuracy for proprioceptive localization of a body part has been to ask participants to reach to the location of the body part (e.g. a hand or a foot). However, as reach planning also incorporates proprioceptive information derived from the end effector, a reach task may not elicit a true measure of one's ability to localize a proprioceptive target; reach errors may reflect kinematic aspects of the reaching hand and not necessarily localization error. As such, reach tasks may not be the best way to measure proprioceptive localization accuracy. In addition, Dijkerman and de Haan (2007) have suggested that proprioceptive processing for perception and proprioceptive processing for action are represented differently in the CNS. Consistent with visual processing for perception and action (Goodale and Milner 1992), their model highlights two pathways: a perception pathway projecting from the anterior parietal cortex (APC) to the posterior insula and posterior parietal cortex (PPC) through the secondary somatosensory cortex (S2) (Mishkin 1979), and a second pathway, representing action information, projecting from APC through S2 to the PPC. Overall, previous localization tasks may elicit variations in measured accuracy values that are not due to accuracy in identifying proprioceptive target location (e.g. dominance of the reaching hand). As a means to circumvent these issues and explore proprioceptive localization directly, we examined the accuracy with which participants localized a part of the body (the hand) for perception (i.e. making a perceptual judgment about a hand's location in space relative to a visual or proprioceptive reference), and for action (i.e. reaching to the target hand). We also examined the effects of active and passive movement of the target hand on localization accuracy and compared localization accuracy across the two hands.

Our first aim was to examine participants' ability to localize a part of their body without the intended action to reach to that body part, and to compare these errors to errors achieved when participants reached to the same body part. In our proprioceptive estimation task participants made perceptual judgments about the location of their hand relative to visual references, or their body's midline. Specifically, on each trial, participants indicated whether their hand was to the left or right of a visual reference or their body's midline (a proprioceptive reference). The proprioceptive representation of the center reference location (body midline) was included to determine if any observed inaccuracies in participants' estimates of felt hand location relative to references were due to comparing the location of stimuli from different modalities rather than the same modality. In addition, given that some previous studies have shown differences between visually-guided and proprioceptive-guided reaches (e.g. Sarlegna and Sainburg 2007), we used both visual and proprioceptive references for perceptual comparisons. In this condition, placement of the target hand was also either active (participants actively placed their hand in the target location by pushing a robot manipulandum along a constrained path from a start location to a target location), or passive (the robot manipulandum positioned participants' target hand). We were then able to compare participants estimates of unseen hand location in this proprioceptive estimation task (perceptual task) with a proprioceptively guided reaching task, in which participants reached to the felt location of their unseen target hand (action task).

Our proprioceptive estimation task is different from previous tasks used to assess proprioceptive localization accuracy in that participants were not asked to plan or perform a goal directed movement to the target hand. Instead, participants made a perceptual judgment about the location of their hand relative to visual or proprioceptive references. Since making an estimate of where your unseen target hand is relative to a reference (perceptual judgment) may require different processing of proprioceptive information than when planning and executing a reach to the unseen target hand (Dijkerman and de Haan 2007), we first hypothesized that the pattern of errors observed in our proprioceptive estimation paradigm may differ from those detected when participants were asked to reach to their unseen target hand.

In both the proprioceptive estimation task and proprioceptively guided reaching task, participants were asked to localize both the dominant (right) and nondominant hands. Research has suggested dominant–nondominant asymmetries in movement control processes. For example, right handed participants have been shown to exhibit faster reaction times when reaching with the left hand than when reaching with the right hand, but that they also tend to reach more accurately with the right hand than with the left hand (Boulinguez et al. 2001), suggesting a trade off between the speed of the reaching movement and the accuracy of the reaching movement (Fitts 1966). In addition, Wang and Sainburg (2007) examined the effect of arm/hand dominance on reach performance in right handed participants by dividing participants into one of two reaching task groups. Participants in the first reaching task group reached from one start location to three target locations first with one hand then with their other hand. Participants in the second reaching task group reached from three start locations to one target location, once again, with one hand followed by the other. Their results revealed that participants' reaches were more accurate and less variable when reaching with the dominant hand/arm in the one start location-three target locations condition. Conversely, when reaching with the nondominant hand/arm, participants' reaches were more accurate and less variable in the three start locations-one target location condition. Wang and Sainburg (2007) suggested that there may be dominant arm system advantages in controlling aspects of movement planning (e.g. direction of the movement) and nondominant arm system advantages in controlling aspects of movement execution (e.g. correction and control of the limb during the movement). To date, however, it is unclear whether such dominant–nondominant hand/arm asymmetries are unique to reaching tasks or if they would arise in a more perceptual task, as in our proprioceptive estimation paradigm. For example, Goble et al. (2006) found that right handed participants were more accurate in proprioceptive matching of elbow angle when matching with their nondominant left arm than when compared to their dominant right arm. A joint angle matching task may be more perceptual than a reaching task. As such, our second aim was to determine if the pattern of errors in each of our tasks (our perceptual proprioceptive estimation task and our motor proprioceptively guided reaching task) would differ as a function of the dominant versus nondominant target hand.

Previous research on proprioceptive localization in reaching tasks has also suggested that participants are better at localizing a body part after it has been actively placed compared to after it has been passively positioned (e.g. Paillard and Brouchon 1968; Adamovich et al. 1998; Laufer et al. 2001). Laufer et al. (2001) found that when participants reached to the remembered location of their right hand, they were less accurate in their estimation of hand location when it was passively moved to a target location, than when it was actively moved to a target location. This difference between passive and active positioning was found even when participants received visual information about the target hand during its movement to and from the target location. Our third aim was to determine if movement of the target hand (i.e. active or passive placement) in our perceptual paradigm would have a similar effect as that previously observed in reaching paradigms.

Methods

Subjects

In total, 63 healthy, right-handed university students (ages 17–36 years) were recruited to participate in this study. All subjects were pre-screened verbally for self-reported handedness, and history of visual, neurological, and/or motor dysfunction. All subjects gave informed consent, and the study was conducted in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee. Half of these participants received course credit for their participation, while the remainder was composed of volunteers in ours, and neighboring labs.

General experimental setup

A side-view of the setup is illustrated in Fig. 1. In all experiments, subjects were seated at a table. The distance of the chair from the table and the height of the chair were adjusted in order to ensure that subjects could comfortably see all reference marker positions, or comfortably reach to their unseen target hand in the target positions. Subjects were instructed to grasp the vertical handle of a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) under an occluding platform with their unseen hand in such a way that their thumb (of either the right or left hand) rested on top of the robot handle (1.4 cm in diameter); the handle was at approximately waist level. During the experiments, the robot manipulandum either moved the hand passively, in a single direction to a specified location, or restricted participants' active movement along a straight constrained path, or slot, until the hand reached the target location (Fig. 2d). For the constrained path, the robot generated a resistance force [proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm s)] perpendicular to the slot (see Henriques and Soechting 2003; Wong and Henriques 2009).

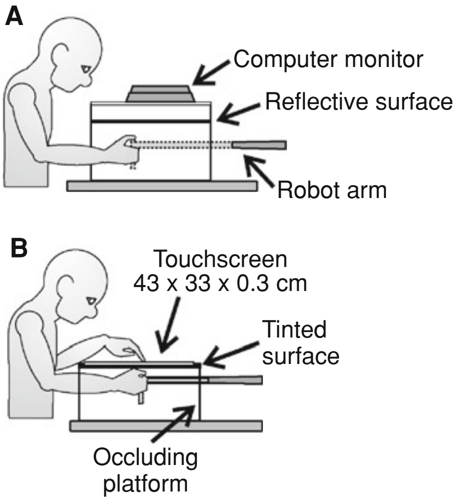

Fig. 1 Schematic of the experimental setup. **a** Side-view of the experimental setup used for the proprioceptive estimation experiments. **b** Side view of the experimental setup used in the proprioceptive-reaching experiment

Participants could not see their target hand or forearm during the experiments, as it was hidden by an occluding platform. In addition, a black cloth, draped between the experimental setup and the subject, was used to cover the remainder of their target arm up to the shoulder. The surface of the occluding platform was tinted and reflective, and could not be seen through unless illuminated from below. Subjects could only see the location of their target hand for those experiments where eight white LEDs, positioned on the underside of the occluding platform, illuminated the target hand.

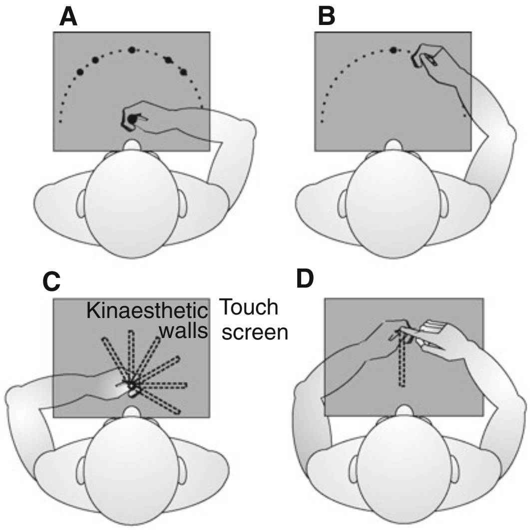

Fig. 2 Above view of the experiment surface and the stimuli locations for the proprioceptive estimation experiments (**a** and **b**) and proprioceptive-reaching experiments (**c** and **d**). **a** In the proprioceptive estimation experiments, the locations of the alignment reference markers are indicated by *solid black circles*, and were located along a arc (45° and 30° left and right of the midline or 0° reference marker) at a distance of 10 cm from the home position. The home position was represented by a 10 cm *green circle* (shown as a *solid black circle* above the target hand in **a**). In all these experiments the 0° reference marker (along the midline) was represented proprioceptively, as well as visually, for a total of six reference markers for the proprioceptive estimates. **b** On each trial in the proprioceptive estimation experiments, participants' target hand would be actively or passively moved from the home position to a location along the arc (*dotted line*) so that it would either be to the left (CCW) or right (CW) of a reference marker; the marker appeared only after the hand was placed in its final location. Participants were asked to indicate if the felt position of their hand was to the left/CCW or right/CW of the visible reference marker (*solid black circle* in figure). **c** Schematic of the kinesthetic paths to the target sites used in the proprioceptive-reaching experiment. **d** On each trial of the proprioceptive-reaching experiment, once the target hand was in the target position, participants were asked to reach with the opposite hand to the felt location of the target hand

Proprioceptive-estimation experiment

In this experiment, visual stimuli were projected from a monitor (model: Samsung 510N, refresh rate: 72 Hz) installed 17 cm above the robot, and viewed by subjects as a reflected image on the reflective surface of the occluding platform (Fig. 1a). The images displayed by the monitor appeared to lie in the same horizontal plane as the robot handle.

Proprioceptive-reaching experiment

In this reaching experiment, a 43 × 33 cm, 3 mm thick touch screen panel (Keytec Inc., Garland, TX, USA) was placed on top of the occluding platform in such a way as to minimize the distance from the top of the manipulandum, and the subject's target hand, to the surface of the touch screen to 28 mm (Fig. 1b). The touch screen recorded the location where the visible reaching hand made contact to indicate the position of the unseen target hand below.

General procedure and stimuli

Proprioceptive-estimation experiments

We conducted three experiments to assess the acuity of participants' proprioceptive estimate of their unseen hand position relative to reference markers. In experiment one (active estimates-right hand), participants moved their right hand along a robot-generated constrained path from a start location to a target location. In experiment two (passive estimates-right hand), participants' right hand was passively moved to the target site by the robot-manipulandum (movement time 400 ms, average speed 26 cm/s). Lastly, in experiment three (active estimates-left hand) participants moved their left hand along a robot-generated constrained path from the start location to a target location. Only active movement of the left hand was used as we found no significant difference between active and passive placement of the right hand between experiments one and two.

All trials began with the robot positioned at a home position located directly in front of the subject's midline. In all three experiments the reference markers were arranged along a circular radius, or arc. One reference marker was located 10 cm directly in front of the home position (central reference marker; Fig. 2a). This reference was represented both visually, using a yellow disk (1 cm in diameter), and proprioceptively, using participants' internal representation of body midline. In addition, four other visible reference markers were used. They were also 10 cm from the home position, located 30° and 45° left and right of the midline. Ten subjects participated in each of the three experiments.

At the beginning of each trial, subjects were made aware of the starting position of their hand by the presentation of a green disk (1 cm in diameter) projected directly above their hands (depicted by a solid black circle above the target hand in Fig. 2a). The hand was then passively or actively moved out along a straight path. At the end of the movement (defined by either the robot stopping or the robot-generated path ending), a visual reference marker appeared (Fig. 2b), or a beep would indicate the reference as the participants' body midline. Participants then reported whether the felt location of their unseen hand was to the left or right of the reference marker (two-alternative forced choice).

In order to determine the location at which subjects felt their hand was aligned with a reference marker, we adjusted the location of the hand with respect to each reference marker over trials using a two-alternative forced choice (2-AFC) adaptive staircase algorithm (Kesten 1958; see Treutwein 1995 for a review). For each reference marker there were two corresponding staircases, a left and right, which were adjusted independently and randomly interleaved. Each staircase began such that the hand was 20° to the left or right of the reference marker. The hand was always positioned at a radial distance of 10 cm from the home position, and hence on the same circular arc that joined all reference markers, before a reference marker appeared (dotted line in Fig. 2a). The position of the hand was then adjusted over trials depending on the subject's pattern of responses using the adaptive algorithm. If participants associated a specific felt location with a given reference marker, the two staircases converged toward a certain angle at which subjects had an equal probability of reporting left or right.

Participants were instructed that the reference markers were positioned along a circular arc and that their responses were to be based on the felt position of their hand along this arc with respect to the reference marker. There were no time constraints during the task, and subjects were encouraged to take as long as they needed before pressing a left or right arrow key on a keyboard to indicate whether they felt their hand to be to the left or right of the reference marker, respectively. After entering a response using the left or right arrow keys, the reference marker disappeared and the target hand was returned to the start location to begin the next trial. In the passive condition, the robot returned participants' target hand to the start location and in the active conditions, participants actively returned their hand to the start location, guided by the robot.

As previously mentioned, the central reference markers were represented visually or proprioceptively. On proprioceptive reference marker trials, a subject's hand was moved outwards (either passively or actively) and a beep sounded at the end of the movement. This cue signaled participants to indicate if their hand was either to the left or right of their body's midline. In all other aspects these trials were identical to those in which a visual reference marker was displayed. On trials where the central reference marker was visual, subjects were not made aware that this reference marker was located directly in front of their midline.

In all experiments, subjects made 50 judgments for each of the six reference markers for a total of 300 trials. Trials were pseudo-randomized. Specifically, in order to ensure that the visual representation of the central reference marker did not influence performance on trials in which the same reference marker was proprioceptive, staircases corresponding to the central proprioceptive reference marker were presented in the first half of the testing block, and staircases corresponding to the central visual reference marker were presented in the second half of the testing block. In the first half of each testing block, the central reference marker was presented twice and each peripheral reference marker was displayed once every six trials. One testing session lasted approximately an hour.

Proprioceptive-reaching experiments

We also completed two experiments to assess participants' accuracy when reaching to a proprioceptive target (a hand) located in one of six locations. In the first reaching experiment, the left hand was used as the proprioceptive target, and subjects reached to its unseen location with their visible right hand (12 participants; Fig. 2d). In the second reaching experiment, the right hand was used as the target for the reaching left hand (21 participants). The locations of the proprioceptive target were the same for the left hand and the right hand. Specifically, all target locations were 12 cm from the home position, one directly in front (along the midline), one 30° counter clock-wise (CCW) and the others 30°, 60°, 90° and 120° clockwise (CW) from the midline (corresponding to the end of the dashed slots in Fig. 2c). Like in the active versions of the Proprioceptive-estimation experiment, subjects moved the target hand out along a robot-generated pathway, or slot to the final target site. The room was dimly lit enabling subjects to see their reaching hand, but not the covered target hand.

At the beginning of each trial white LEDs were illuminated beneath the occluding platform, allowing subjects to see the initial position of the target hand. Participants first reached to the seen position of the thumb of their target hand with the seen index finger of their reaching hand by touching the touch screen directly above the seen position of the target thumb. Once the subject reached to the location on the touch screen to indicate the seen start position of their target hand, the LEDs turned off so that the target hand was no longer visible under the occluding platform. Participants then moved their target hand along one of six randomly selected slots to a target location at the end of the groove (Fig. 2c, d). Once their target hand reached this target location at the end of the robot generated slot, participants reached to its unseen location with their opposite hand by again placing their index finger on the touch screen at the location where they felt their unseen target hand to be (Fig. 2d). Once the reach was completed, a beep indicated that the touchscreen registered the reach. Subjects were then to return their reaching hand to the table, and move the target hand back along the same slot towards the start location. The position of their target hand was again illuminated by the LEDs when it was 2 cm from the origin. When subjects reached the origin, they were asked to reach to where they saw their target hand (their thumb resting on top of the robot handle) to initiate the next trial. Participants completed ten reaches to the target hand at each target site for a total of 60 trials. The experiment took approximately 10 minutes to complete.

In order to establish a baseline measure for reaching accuracy, at the end of each experiment, we had subjects reach to the target hand at each target location while the target hand was illuminated during the entire reach (i.e. they reached to the seen location of their target hand).

Data analysis

Proprioceptive-estimation experiments

To obtain estimates of the location at which subjects felt their hand was aligned with a given reference marker (i.e. the angle at which subjects reported left and right equally often), we fitted a logistic function to the data for each reference marker in each experiment (e.g. six estimates were computed for each subject in each experiment). Based on each logistic function, we then calculated the bias (the point of 50% probability, represented as circles in Fig. 4) and uncertainty (the difference between the values at which the response probability was 25 and 75%, shaded region in Fig. 3) for each reference marker, where bias is a measure of the accuracy of hand-reference marker alignment, and the magnitude of the uncertainty range defines its precision. Bias and uncertainty related to a particular reference marker were excluded if the associated uncertainty was greater than mean uncertainty across all reference markers within the experiment + 2 standard deviations (in total 21 (or 5.8%) hand-reference marker estimates were excluded).

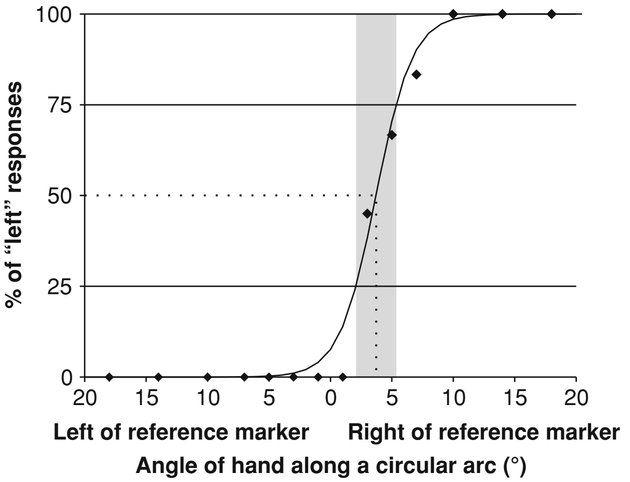

Fig. 3 An example of bias and uncertainty range calculation using data obtained from a single subject for one reference site. For each location of the target hand relative to the visual reference, the solid diamonds indicate the percentage of times the participant indicated their target hand was to the left of the reference. In order to determine the angle at which subjects perceived their hand was at the reference marker, we used an adaptive staircase procedure in which subjects reported if the felt position of their unseen hand was to the left or right of a reference marker. We then fit a logistic function to the data to define bias and uncertainty, where bias is the probability of reporting left or right equally often (50%, indicated by the *filled circle*) and uncertainty is the difference between the values at which the response probability was 25 and 75% (region indicated by the *shaded rectangle*)

To compare the bias and uncertainty results achieved across active and passive estimates of right hand position, we conducted a two-way repeated measure ANOVA (RM ANOVA), with the reference marker location as the second factor. In a second analysis, we compared results achieved for active right and left hand positioning using a two-way RM ANOVA, with reference marker location as the second factor. All ANOVA results are reported with Greenhouse-Geisser-corrected p values. Differences with a probability less than 0.05 were considered to be significant. Tukey's Honestly Significant Difference (HSD) post hoc tests were administered to determine the locus of these differences ($\alpha = 0.05$).

Proprioceptive-reaching experiment

Reaching errors were calculated by taking the finger position, as recorded by the touch screen, for each reaching trial, and subtracting the baseline finger position (one reach for each target location made to the seen target hand at the end of each experimental session) for each of the six target locations. To assess the effect of target hand and target location on participants horizontal reach errors, a two-way RM ANOVA was conducted. Also, to measure precision of the reaches for each target location, we fitted 68% confidence interval ellipses for the reach endpoints made to each target for each subject. A one-way ANOVA was then used to compare the area of these ellipses among target locations.

Results

Proprioceptive-estimation experiments

If subjects correctly perceived that the felt position of their hand matched the visual or proprioceptive reference marker when their hand was directly underneath the reference marker, the observed biases would have been zero (falling on the reference markers (solid diamonds) in Fig. 4a–c and along the horizontal lines in Fig. 4d–f). From Fig. 4 we see that this was not the case. Figure 4a–c displays mean biases (indicated by open circles for visual references, and the solid circle for the proprioceptive reference of participants' body midline) in x–y coordinates relative to each reference marker for each of the three paradigms. That is, for the active left hand condition (A), for the active right hand condition (B), and for the passive right hand condition (C). The angular difference between these mean biases (open and solid circles) and each reference marker (solid diamonds) for each of these conditions have been plotted in Fig. 4d–f.

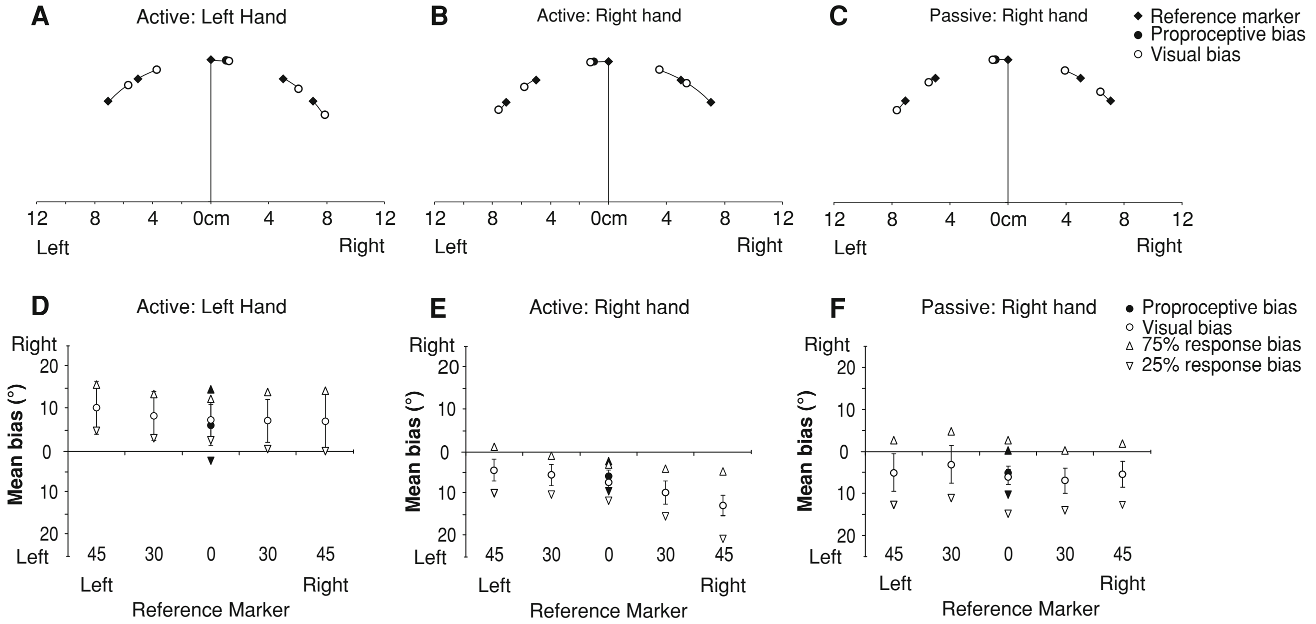

Fig. 4 Mean biases at each reference marker for all three Experiments ((**a** and **d**) active: left hand, (**b** and **d**) active: right hand, (**c** and **f**) passive right hand). The top row of panels (**a**–**c**) represent an above 2D view of the proprioceptive biases (*circles*) and the location of the corresponding reference marker location (diamonds, joined by a solid line). The bottom row of panels (**d**–**f**) plot the angular difference between the proprioceptive estimates or biases (diamond) and the reference marker locations (indicated as 0° in this plot) for each reference location. Biases for the visual reference markers are indicated by the *open circles* while biases for the proprioceptive reference markers are represented by the *filled circles*. *Error bars* reflect standard error of the mean across subjects. The *triangles* (**d**–**f**) indicate the mean uncertainty ranges for each reference marker, with upright triangles indicating the hand location that subjects reported was left/CCW of the reference marker 75% of the time while upside-down triangles indicating the same for the right/CW direction. The filled triangles at the centre reference marker correspond to the proprioceptive reference marker

In general, participants misperceived the position at which their hand was aligned with a reference marker. They judged their right hand to be in the same position as the reference marker when it was slightly to the left of the marker (as seen by the leftward biases in Fig. 4b, c, e, f), and their left hand to be in the same position as the reference marker when it was slightly to the right of a marker (as seen by the rightward biases in Fig. 4a, d). One sample *t* tests for the right and left target hands revealed that participants' biases differed significantly from zero (with Bonferroni correction, $p < 0.025$).

Right hand

If we compare across Fig. 4b, c, e, f, we see that there is no difference in participants' estimates of right hand-reference marker alignment when the robot passively positioned their limb (Mean bias 5.27 ± 9.92° or about 0.92 ± 1.74 cm; 4c) compared to when subjects actively moved the robot to the same location (Mean bias 7.45 ± 7.40° or about 1.3 ± 1.29 cm; 4b), $F(1,18) = 1.520$, $p = 0.234$). Furthermore, we also found that participants' biases were independent of the location or type of reference marker ($F(5,90) = 1.014$, $p = 0.356$). In other words, participants had a similar bias when perceiving the position of their right hand relative to a reference marker, regardless of the locations of these markers or whether the marker was visual or proprioceptive (open or closed circles at centre 4b, c, e, and f).

In Fig. 4d–f, we indicate the boundaries of the mean uncertainty range at each reference marker with triangles (the uncertainty range is the difference between the values at which the response probability, for a choice of *left*, was 25 and 75%). Upward pointing triangles represent the locations of the hand that participants' responded to as left of the reference marker 75% of time and downward pointing triangles indicating those positions of the hand participants responded to as right of the reference marker 75% of the time. At the centre reference marker, the open triangles refer to the visual marker and the filled triangles correspond to the proprioceptive marker. Participants displayed similar levels of precision (mean uncertainty range was 14.5° or about 2.5 cm) regardless of how their target hand was positioned ($F(1,18) = 3.549$, $p = 0.076$) or of the location of the reference marker ($F(5,90) = 2.085$, $p = 0.108$).

Left hand

Figure 4a and d display the mean biases (indicated by an open circle for visual reference markers and a solid circle for the proprioceptive reference of participants' body midline) for participants' judgments of the actively placed left hand location relative to the references.

The mean bias for the left hand (active) was on average, 7.7° right (or about 1.4 cm) of a reference marker. The biases when estimating the location of the left hand relative to the reference markers differed from those of right hand ($F(1,18) = 17.948$, $p < 0.001$), although the magnitude of the errors for each hand was similar, just in different directions. The hand-dependent biases, for either hand, did not vary significantly across target direction ($F(5,45) = 0.215$, $p = 0.954$), suggesting that the pattern of biases for the different locations were similar across the two hands, and only shifted between hands. Participants also displayed similar levels of precision (mean uncertainty range was 12.7° or about 2.2 cm) regardless of the location or type of reference marker ($F(5,45) = 0.788$, $p = 0.476$).

The magnitude of the uncertainty range when participants estimated the location of their left hand relative to the reference markers did not differ from when participants estimated the position of their right hand relative to reference markers ($F < 1$).

Proprioceptive-reaching experiment

Figure 5 displays reach end point errors, averaged across subjects, when the left hand was the target (a) and when the right hand was the target (b). The dashed lines between target location (crossed circles) and mean reach endpoint (squares) show displacement error, or the average directional difference between the target locations and reach endpoint locations. The pattern of reach error did not differ between the target hands ($F(1,11) = 2.47$, $p = 0.144$); participants consistently overshot the target relative to the start position. The magnitude of the displacement errors did vary as a function of target location for the two hands ($F(2.58, 28.47) = 14.46$, $p < 0.05$). Analysis revealed that reaches were the least displaced overall when the target hand was in the far most CW target location (120° CW, 20.29 ± 1.62 mm, $p < 0.05$); less displaced in this location than when the hand was in the strictly rightward (90° CW) target location (31.45 ± 3.45 mm, $p = 0.08$) relative to the start position. Yet these errors were largest for the 60° CW target location (43.66 ± 4.8 mm), more displaced in this position when the hand was in the 0°, 90° CW, or 120° CW target locations ($p < 0.05$).

As shown in Fig. 5c these overshoot errors were also directed more CCW or leftward overall when the target was the left hand (circles), but more CW or rightward when the target was the right hand (squares), ($F(1,11) = 28.46$, $p < 0.05$). Moreover, these mean angular reach errors varied significantly as a function of target location ($F(3.70,40.72) = 3.03$, $p = 0.03$). A significant interaction between target hand and target location ($F(3.7,40.72) = 3.03$, $p < 0.05$) highlighted the greater CCW estimates of the left hand target than the right hand target in all target locations ($p < 0.05$) except the 30° CCW target location ($p = 0.09$). The overall pattern of errors was similar across the two hands; reaches to targets that were in front of subjects were deviated less CW than reaches made to rightward/CW targets.

To measure the precision of the reaches for each target location, we fitted 68% confidence interval ellipses for each subject for reach endpoints made to each target. These ellipses are shown in Fig. 5a and b. Precision of reaches made to the left hand target (mean ellipse area of 257.8 mm^2) tended to be poorer than those made to the right hand target (mean ellipse area of 210.32 mm), although this difference between the hands did reach not significance ($F(1,160) = 3.40$, $p = 0.06$). Reaching precision also varied with target location ($F(5,160) = 2.56$, $p < 0.05$), but only due to a difference between the 0° (midline) and 60° CW targets, with reaches to the latter being less precise than the former. There was no significant interaction between target hand and target location ($F(5,120) = 1.12$, $p = 0.35$).

Discussion

The present study sought to examine the accuracy with which participants localized a part of their body, specifically their left or right hands. While many studies have employed reaching (e.g. Pouget et al. 2002; Blangero et al. 2005) or matching tasks (e.g. Wann 1991), in which a participant reaches to, or matches, the current location of a body part (e.g. the right hand or a foot) using another body part (e.g. the opposite hand), here we considered that the localization of a body part with respect to an external reference may differ from localization of a proprioceptive reach target. As such, we included two separate measures of localization. In our first task, participants judged the location of their left or right hand relative to visual reference markers or a proprioceptive reference of their body's midline. In our second task, participants reached with a seen hand (i.e. either left or right) to the unseen location of the other hand.

Overall, localization of both the left and right hand in our proprioceptive estimation paradigm was biased. Participants indicated that they perceived their left hand to be in the same place as the reference marker when it was to the right of the reference marker, indicating that participants perceived their left hand to be more to the left than it actually was. Their right hand was perceived to be in the same location as the reference marker when it was to the left of

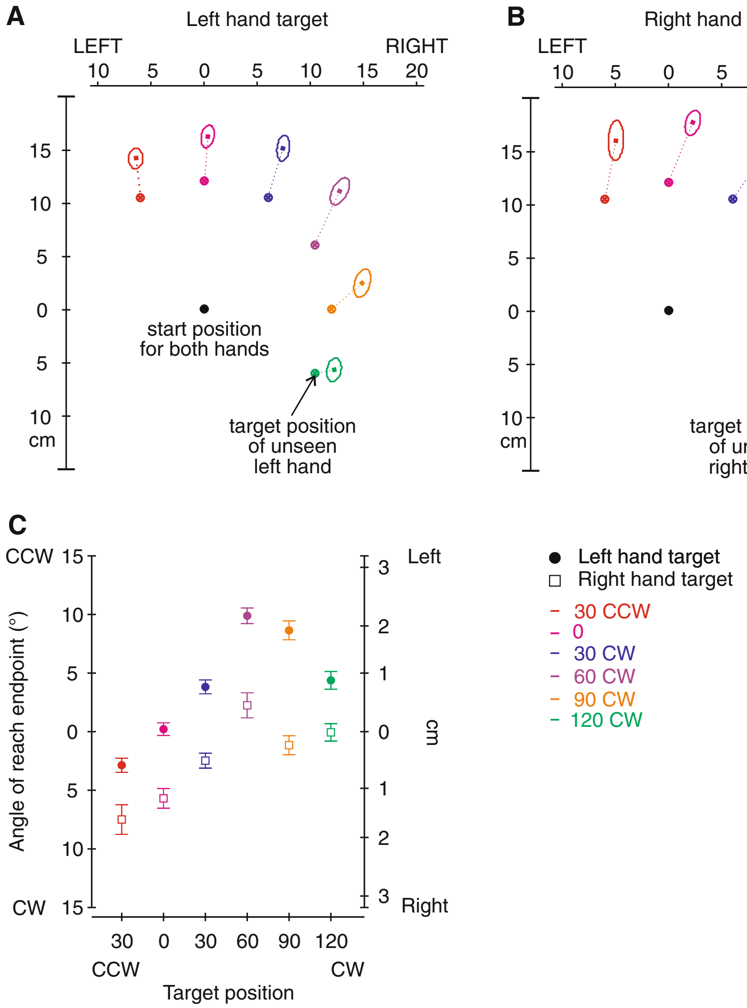

Fig. 5 Reach end points when the left hand was the target **a** and when the right hand was the target **b** broken down by target location (*color* coded). The *dotted lines* between target location (*circles* containing an X) and mean reach endpoint (*solid squares*) display displacement error for each target location. Reach precision is depicted using 68% confidence ellipses. **c** Average angular error plotted as a function of target location for each hand (*circles* for left hand target and *squares* for right hand target)

the reference marker, suggesting that participants perceived their right hand to be more rightward than it actually was. While these biases are opposite in direction, they were similar in magnitude across the left and right target hands and across reference marker locations in the workspace. Also, the magnitude of the uncertainty ranges (precision) did not differ between the left and right target hands and there was no effect of active versus passive placement of the target hand on localization accuracy or precision for the right hand.

In our proprioceptive-guided reaching task, reaches made to the left target hand were deviated more CCW overall (3.96 ± 6.00°) than reaches made to the right target hand, indicating that participants tended to perceive their left hand to be more leftward/CCW than it actually was. The mis-reaches to the location of their right hand were shifted more rightward/CW in comparison (2.42 ± 4.94°). Interestingly though, the pattern of angular errors across the target locations was similar for the two hands; reaches to targets that were in front of subjects tended to be deviated less CW than reaches made to rightward/CW targets. Also, the precision of reaches varied little as a function of target hand or target location.

Proprioceptive localization: accuracy and precision

The patterns of bias for the left and right hands observed in our proprioceptive estimation task are consistent with those reported in reaching tasks (Crowe et al. 1987; van Beers et al. 1998; Haggard et al. 2000). These studies have reported that, when reaches are made to the right hand using the left hand, participants overestimate the horizontal location of the right hand, reaching too far to the right, and when reaches are made to the left hand using the right hand, participants overestimate the horizontal location of the left hand, reaching too far to the left. This pattern of reaching errors would be expected if participants truly misperceived the location of their right hand (or left hand) to be more to the right (or left) than its actual location. Although we did not find as large of an overestimation in target hand location along the azimuth in our reaching paradigm, we did find that reaches made to the left hand using the right hand were, overall, deviated to the leftward/CCW direction and reaches to the right hand using the left hand were deviated more to the rightward/CW direction. As our proprioceptive estimation paradigm did not require localization of the target hand using a reach, these biases suggest that overestimation errors along the azimuth are not due to the reaching hand or planning of a reach. In the absence of vision of the hand, these biases could be due to a misperception of hand location relative to the body midline (e.g. Ghilardi et al. 1995).

Previous studies have shown asymmetries in joint matching (Goble et al. 2006) and proprioceptive-guided reaching (Haggard et al. 2000) across the two hands. For example, while Goble et al. (2006) found that participants were more accurate in their proprioceptive matching of elbow angle when matching with their nondominant left arm compared to their dominant right arm, Carson et al. (1990) found no spatial location matching advantages across the two hands when participants were asked to reproduce the spatial location of their seen or unseen left or right index finger using the same or opposite finger. For proprioceptive reaching, Haggard et al. (2000) found that reaches to the right hand were more accurate than reaches to the left, suggesting perhaps left hemisphere dominance for proprioceptive localization, or at least perhaps a better estimate of hand position for the dominant hand. Like Carson et al., we found that participants' estimates of hand location were similarly accurate across the two hands in both of our paradigms, although errors were opposite in direction, suggesting that there may not be asymmetries in proprioceptive information processing across the brain hemispheres, at least for some tasks (Hodges et al. 1997).

The accuracy (Haggard et al. 2000) and precision (van Beers et al. 1998) of proprioceptive-guided reaching has also been shown to depend on the location of the target in the workspace. In our proprioceptive-guided reaching paradigm, participants' reaches to the 120° CW target location were more accurate than reaches to the 90° target location (across target hands) and reaches to the 60° CW location were least accurate overall. However, we found no target dependent effects in our proprioceptive estimation paradigm. For proprioceptive reaching, van Beers et al. (1998) have suggested that reaches made to locations along the rotational axis of the target shoulder tend to be more precise. We found that the magnitude and pattern of scatter of proprioceptive reaches did not vary much across target directions for either hand. Uncertainty ranges in our proprioceptive estimation task did not differ at all across target locations. Overall our results do not suggest such a direction and location-dependent difference in proprioceptive localization accuracy or precision. Specifically, there appears to be very little systematic change across target locations for both the bias and uncertainty ranges in our proprioceptive estimation paradigm and the displacement error and the size or shape of the ellipses in our proprioceptively guided reaching paradigm. However, in our proprioceptively guided reaching paradigm, we may not have enough reach endpoints for each of our six target sites to really investigate this possibility (van Beers only tested three target sites, with the right hand as the target). Since we likewise found no difference in precision for the proprioceptive estimation task, it is possible that the existence of location-dependent sensitivity of proprioception may be depend on the task, the hand tested and the size of the workspace.

Separate processing for proprioceptive information

Similar to visual processing (Goodale and Milner 1992; Milner and Goodale 1995), proprioceptive information may be processed differently depending on whether that information will be used for action or for perception (Dijkerman and de Haan 2007). More specifically, Dijkerman and de Haan (2007) have suggested that proprioceptive processing for perception and proprioceptive processing for action may be represented differently in the brain. As previously mentioned, their model highlights a perception pathway projecting from the APC to the posterior insula and PCC through S2 and a second pathway, which represents action information, from APC through S2, to the PPC. This model also highlights processing differences between information derived from being touched and information derived from touching external objects, as well as different levels of processing such as identifying where on the body a touch has occurred as compared to the more complex processing of touch direction or speed. The results of our two paradigms suggest that the magnitude or pattern of errors for our more perceptual (proprioceptive estimation) task did not differ substantially from those during our action (proprioceptive-guided reaching) task. In contrast, our results may suggest that the errors in the localization of a limb, may carry over to errors made when reaching. However, one-way that our proprioceptive estimation paradigm differs from previously published proprioceptive-guided reaching paradigms (e.g. Adamovich et al. 1998; Laufer et al. 2001) is that we did not find differences between our passive and active placement conditions. This difference may have to do with how people indicated the felt location of their target hand in this task and supports the idea that proprioceptive information processing may differ depending on its eventual use (Dijkerman and de Haan 2007). Perhaps the additional information derived from active movement (e.g. efference copy of a motor command) is not needed when the proprioceptive information is used to simply perceive or monitor the location of a body part. Mishkin (1979) and Dijkerman and de Haan (2007) have suggested that proprioceptive information used for perception is processed within a pathway that terminates in the posterior insula, an area known to contribute to aspects of body awareness such as introspective monitoring of body functions (e.g. determining one's heart rate) and homeostasis.

Conclusions

This preliminary study presents a novel method for the measurement of the accuracy with which humans localize their unseen hands. Our proprioceptive estimation paradigm differs from previous methods in that participants did not use a goal directed action to indicate the felt location of their hands. Furthermore, both of our paradigms also examined localization of the right *and* left hands in right handed participants.

In the proprioceptive estimation paradigm, we observed biases in participants' estimates of left and right hand locations that were consistent with horizontal overestimations of hand location observed in previous reaching paradigms. However, the movement of the target hand (active or passive) in this paradigm did not affect participants' estimates of target hand location. In our proprioceptive-guided reaching paradigm, we observed a similar pattern of biases in hand localization such that participants judged their left hand to be more leftward or CCW than it actually was, and more leftward than the right hand. While we present novel findings concerning a new localization procedure and a preliminary comparison between this proprioceptive estimation task and a proprioceptive-guided reaching paradigm, further experiments are needed with a better comparison with standard reaching tasks to truly assess proprioceptive sensitivity.

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