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A task-dependent effect of memory and hand-target on proprioceptive localization

Stephanie A.H. Jones[a,b], Katja Fiehler[c], Denise Y.P. Henriques[a,d,*]

[a] Centre for Vision Research. York University, Toronto, Canada
[b] Department of Psychology, York University, Toronto, Canada
[c] Justus-Liebig-University Giessen, Giessen, Germany
[d] School of Kinesiology and Health Science, York University, Toronto, Canada

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ABSTRACT

We examine whether the task goal affects the accuracy and precision with which participants can localize an unseen hand. Proprioceptive localization was measured using three different tasks: two goal-directed movement tasks (reaching to and reproducing final hand-target location) and a perceptual estimation task in which participants judged the location of the hand-target relative to visual references. We also assessed whether proprioceptive localization in these different tasks is affected by localization from memory, the hand-target being localized (left or right) or the movement path of the proprioceptive target (9 paths, derived from combinations of starting and final hand-target positions). We found that participants were less precise when reaching from memory, but not when reproducing or estimating remembered final hand-target location. Participants also misperceived the felt location of their hands, judging their left hand to be more leftward and their right hand to be more rightward when reaching to and when estimating final hand-target location, but not when reproducing hand-target location. The movement path of the proprioceptive target did not affect localization, regardless of the task goal. Overall, localization seems poorer when proprioception is used to guide a reach with the opposite hand, particularly from memory, and best when merely reproducing the proprioceptive target site. This may have an important application in neuro-rehabilitation, whereby one task may better establish or re-establish important or failing sensory connections.

Proprioceptive localization, or the accuracy and precision with which we can localize a body part in space using proprioceptive inputs, is an important component in the completion of our daily activities and our overall quality of life. For example, patients who have lost somatosensory input about limb position often exhibit difficulties performing single (Nougier et al., 1996), multi-joint (Mechsner, Stenneken, Cole, Aschersleben, & Prinz, 2007; Sainburg, Poizner, & Ghez, 1993) and compensational movements (Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006; Tunik et al., 2003) as well as maintaining posture (Blouin, Teasdale, & Mouchnino, 2007). Therefore, it is important to understand how the central nervous system (CNS) processes and uses proprioceptive information about limb position.

Research has suggested that the task goal may affect proprioceptive localization, perhaps changing the value assigned to proprioceptive information or the way it is used by the CNS (Dijkerman & de Haan, 2007). That is, the processing of proprioceptive information when it is used to guide a goal-directed movement (e.g. a reach) may differ from the processing of proprioceptive information for perception of the position of a limb in space (e.g. relative judgement of hand position). However, previous studies have generally employed a single task for measuring proprioceptive localization (Goble & Brown, 2010; Goble, Noble, & Brown, 2009; Jones & Henriques, 2010; Laufer, Hocherman, & Dickstein, 2001; van Beers, Sittig, & Denier van der Gon, 1998; Wilson, Wong, & Gribble, 2010), with few exceptions (Jones, Cressman, & Henriques, 2010) and there have been few attempts to consolidate the existing literature in which a wide variety of proprioceptive localization measurement methods and paradigms have been used (e.g. Jones et al., 2010). As such, little is known about how the way proprioception is used (i.e. the task goal) affects sensitivity in locating a target body part, or how specific task parameters affect localization across these different tasks. This was the aim of the current study.

1. Task goal

We sought to examine proprioceptive localization differences as a function of the task goal in two ways. First, we expand on

* Corresponding author at: School of Kinesiology and Health Science, Bethune 357, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3. Tel.: +1 416 736 2100x77215.
E-mail address: deniseh@yorku.ca (D.Y.P. Henriques).

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previous research in our lab that found no differences in proprioceptive localization errors across perceptual (relative judgement of hand position, described later) and reaching tasks (Jones et al., 2010) by newly comparing performance on these two tasks with how well people are able to reproduce unseen hand position. Reproduction of unseen hand location has been commonly used to measure proprioceptive hand-target and joint position sense (Goble & Brown, 2010; Goble et al., 2009), however, it has yet to be compared to other proprioceptive localization tasks. Further, reproduction of opposite unseen hand location has revealed non-dominant arm asymmetries (Goble, Lewis, & Brown, 2006; Goble & Brown, 2008) that do not carry over to reaching or estimation tasks (e.g. Jones et al., 2010) highlighting a possible difference in the way the CNS processes proprioceptive information about the limb in this task. Beyond comparing proprioceptive localization across task goals, we also examine how localization from memory, the hand-target being localized and the movement path of the hand-target affect proprioceptive localization across the reach, reproduction and estimation tasks. In the following, we describe the specific task parameters in more detail.

2. Task goal and proprioceptive memory

Overall, some studies have reported greater absolute reproduction errors with increasing delays in between target removal and localization (Stelmach & Barber, 1970; Stelmach & Wilson, 1970), while others have not (Stelmach & Walsh, 1972; Stelmach, Kelso, & McCullagh, 1976; Walsh & Russell, 1979; Wrisberg & Winter, 1985). More recently, studies that have examined memory guided reaching (Chapman, Heath, Westwood, & Roy, 2001; Jones et al., 2010) have shown that delayed reaches to proprioceptive targets are less accurate than reaches to the online target location. However, since these studies only tested either reproductions with the same hand or reaching with the opposite hand, and further tested different hands (as the target), it is not clear whether the effect of remembered localization is robust, retention is equivalent for the two hands, or whether the effect of memory would be similar between these goal-directed conditions and perceptual estimates of remembered hand position. We therefore examined the effect of localization from memory across our three tasks. In all three tasks, participants localized the proprioceptive hand-target after it was removed from the target location.

3. Task goal and hand-target

Previous research in our lab found lateral misestimates of hand-target location such that participants judged the left hand-target to be more leftward and the right hand-target to be more rightward than their actual locations (Jones et al., 2010). This hand-target bias was found both when participants were asked to reach to the opposite unseen hand-target and when they estimated final hand-target location relative to visual references or the proprioceptive reference of body midline. This lack of differences in accuracy and precision across hand-targets is in contrast to studies reported by Goble and co-workers (e.g. 2006, 2008, 2010) who find consistent non-dominant arm advantages when participants reproduce the remembered location of one hand using the opposite hand (i.e. contralateral joint matching). A differential effect of the hand-target being localized across tasks may reflect differences in the way proprioceptive information about hand position is processed. As such, here we systematically compare the effect of hand-target on localizations across reach, reproduction and estimation tasks, using the same participants and the same experimental set-up.

4. Task goal and hand-target movement path

Behavioural and neurophysiological research has highlighted the existence of both static (i.e. position) and dynamic (i.e. movement) proprioceptive information, indicating both types of information can be used to determine final limb position (Burke, Hagbarth, Lofstedt, & Wallin, 1976; Edin & Vallbo, 1990; Goble, Noble, & Brown, 2009; Imanaka, 1989; Imanaka & Abernethy, 1992a, 1992b; Lonn, Crenshaw, Djupsjobacka, Pedersen, & Johansson, 2000; Sittig, Denier van der Gon, & Gielen, 1985; Smeets & Brenner, 1995). Therefore, variations in the accuracy and precision of proprioceptive localization may occur with changes in the movement path of the hand-target. However, despite previously reported effects of starting location of the proprioceptive target in reproduction tasks (Imanaka, 1989; Imanaka & Abernethy, 1992a) and final proprioceptive target location in reach and estimation tasks (Jones et al., 2010; Wilson et al., 2010), how a combination of starting and final hand-target location (hand-target movement path) affects proprioceptive localization has yet to be examined. Further, as most studies have employed a single proprioceptive localization method, the question of whether dynamic signals about proprioceptive target movement are used to localize that target across all task types has not been examined. We paired three starting and three final proprioceptive target positions to form nine hand-target movement paths. This manipulation allowed us to not only examine the kind of signals the brain uses to derive the position of the proprioceptive target, but importantly, if these signals differ as a function of the task goal.

In summary, we sought to examine whether proprioceptive localization is affected by the task goal, such as localizing a hand-target for an action (reaching and reproductions) as compared to localizing it for perception (estimations). Secondly, we examine if the effects of proprioceptive memory, the hand-target being localized (i.e. left and right) and hand-target movement path are modulated by the task goal.

5. Methods

5.1. Participants

Fifteen participants (9 males) with a mean age of 22.2 years (*range*: 18–27 years) volunteered to participate in the present experiment. As not all participants completed all tasks, comparisons across conditions included 10 out of the 15 participants (who did complete all tasks) whereas comparisons within conditions included all 15 participants. All participants had normal or corrected to normal vision and were right handed (self-reported). Written informed consent was provided by each participant prior to their participation. This experiment was approved by the York University Human Participants Review Subcommittee.

5.2. General experimental setup

Schematics of the experimental set up are presented in Figs. 1 (reach and reproduction) and 2 (estimation). Participants sat on a height adjustable chair in front of a 90 cm high table (Fig. 1A: reach and reproduction tasks and Fig. 2A: estimation tasks). To restrict movement of the head during testing, participants rested their chin on a chin rest located 40 cm above the table top (chin rest not shown in figure). Participants grasped the vertical handle of a two-jointed robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA) with the left or right unseen hand-target in such a way that their thumb rested on top of the robot handle (1.4 cm in diameter). The robot handle was just above waist level (Figs. 1 and 2A). The proprioceptive target was therefore the participants' left thumb, as it rested on top of the handle of the robot. The term hand-target will be used in place of target-thumb. The manipulandum was occluded by a tinted translucent plexiglass platform so that once the room lights were turned off, participants were not able to see their hand-target or forearm. In addition, a curtain was placed over the remaining portion of the participant's target-arm to ensure that no additional visual information concerning hand-target or arm position could be derived at any point throughout the experiment or testing sessions (curtain not shown in figures).

5.3. Proprioceptively guided reaching

When participants were asked to reach to an unseen hand-target, a 43 (length) × 33 (width) × 0.30 (height) cm thick touch screen panel (Keytec Inc.,

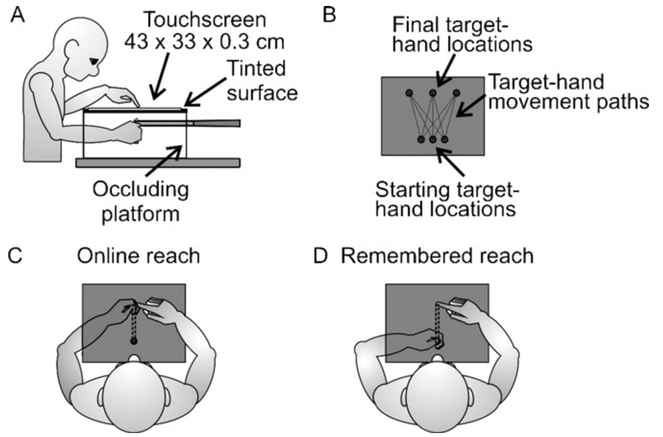

Fig. 1. (A) A side view of the experimental set up used in our proprioceptively guided reach and reproduction tasks. Participants gripped the handle of a robot manipulandum with an unseen hand-target (in this example schematic the right hand-target) and reached to this hand using the seen opposite hand (in this example the left reaching-hand) or reproduced the final hand-target location. A horizontally placed touch screen panel recorded all reach endpoint locations. (B) Start and target positions of the unseen hand-target in our proprioceptively guided reach and reproduction tasks. The robot manipulandum restricted participants' active movement of a hand-target along a straight path to its final position (paths depicted by the dotted rectangles). (C) In the online reach task, participants reached to the felt location of the unseen hand-target using the seen opposite hand. (D) In the remembered reach task, prior to reaching, the hand target was first actively returned to a randomly selected start position. Participants reached to the remembered location of the hand-target (or to where they felt their hand had been).

Garland, TX), with a resolution of resolution of 4096 × 4096 pixels, was used to record reach endpoints (Fig. 1A, C and D). Ambient light from a nearby computer screen allowed participants to see their reaching-hand/arm during the reach tasks. Participants returned their reaching-hand to the same location on the table to the side of their body following each reach. This location was a comfortable location chosen by each participant at the beginning of the experiment. As such, the location that the reaching hand returned to following each reach, although different for each participant, was the same location across all trials for a given participant.

Participants completed two reaching tasks with both the left and right hands serving as the proprioceptive target (four separate 45 min sessions): online reach (Fig. 1C) and remembered reach (Fig. 1D). In all reach tasks, the hand-target began in one of the three start locations (Fig. 1B). On 50% of the trials when the hand-target began in the center start location, the hand-target was illuminated using one white LED. A trial began when participants reached with their seen reaching index finger to the felt or felt and seen (if the hand-target was lit in the center start location) position of the opposite target thumb (resting on top of the robot handle). At this point, if the hand-target began in the lit center start location, the LED turned off so that participants could no longer see the hand-target. The robot manipulandum restricted participants' active movement of the hand-target along a straight constrained path, or slot, from this start location (three start locations located at body midline or 2.5 cm (6°) left or right of body midline, Fig. 1B) to one of the three target locations (37.5 cm in front of the body, at body midline or 5 cm (7.5°) left or right of body midline, Fig. 1B) (see Cressman & Henriques, 2009 for details about active placement of the hand-target). In the online reach condition, participants were prompted one second after the hand-target reached its final location (using an auditory cue) to reach with the seen reaching index finger to the current felt location of the unseen hand-target (Fig. 1C). The hand-target was then actively returned (guided by the robot manipulandum) to a randomly selected start location (hand-target start location for the subsequent trial). Trials in the remembered reach condition were the same as in the online reach condition except that participants first returned the hand-target to a randomly selected start location before reaching to the remembered location of the hand-target (Fig. 1D).

For all reach tasks participants completed 30 reaches for each start (left, center, center lit, and right) and final (left, center, right) hand-target location pairing, for a total of 360 trials. At the end of each experimental session, participants made 10 baseline reaches to the seen hand-target for each start and final target position combination. Reach errors were calculated by taking the reach endpoint, as recorded by the touch screen, for each reaching trial, and subtracting the baseline average reach endpoint for each start and target position pairing. Horizontal reach errors refer to errors in left-right direction. Sagittal reach errors refer to errors in the near-far direction. The precision (or variability) of reaches was examined by fitting 68% error ellipses for the reach endpoints made from each start and final position pairing, for each hand-target, for each subject.

5.4. Proprioceptively guided reproduction task

The experimental set up for the reproduction task was the same as that of the reaching tasks (Fig. 1A). Start and final target locations remained the same as those used in the reach tasks and on 50% of trials when the hand-target began in the center start location, the hand-target was illuminated for one second. Participants completed the reproduction task with the left and right hand-targets (two separate 45 min sessions). On each trial in the reproduction task, the hand-target began in one of the three start positions (Fig. 1B). If the hand-target was illuminated in the center start location, the LED turned off and an auditory cue prompted participants to actively move the hand-target (guided by the robot manipulandum) to one of the three final target locations (Fig. 1B). The hand-target remained at the target location for 1 s before a beep prompted participants to return the hand-target to a randomly selected start position. The hand-target was returned to a randomly selected start position to ensure that participants could not simply replicate the hand movement path. Once the hand-target reached the randomly selected start position, the robot ceased to constrain participants' movement (i.e. participants could freely move the robot within the workspace). Participants were then instructed to move their hand-target back to where the hand-target had been in its final location. For each start (left, center, center lit and right) and final target location combination, participants made 30 reproductions resulting in a total of 360 trials. Horizontal (left–right) and sagittal (near–far) reproduction errors were calculated by comparing the 2D reproduced hand-target position as recorded by the robot manipulandum for each reproduction trial, to the earlier hand-target position in the same trial when the robot guided the hand to the target site. The precision (or variability) of reproductions was examined by fitting 68% error ellipses for the reproduction endpoints made from each start and final position pairing, for each hand-target, for each subject.

5.5. Proprioceptive estimation

A schematic of the experimental set up used in the estimation tasks is presented in Fig. 2. In the estimation tasks, participants were asked to judge the final location of the hand-target relative to visual references. On each trial, participants indicated if the felt position of the hand-target was to the left or right of a visual reference. A computer monitor was used to project a green cursor (1 cm in diameter) representing the hand-target and/or a yellow visual reference (1 cm in diameter) to which participants were asked to compare the felt location of their unseen hand-target (Fig. 2A). The computer monitor was placed face down on a transparent platform (17 cm above the robot handle) so that the image on the computer screen reflected onto the tinted platform below (8.5 cm above the robot handle) (Fig. 2A). In this way, the projected images of the cursor and visual references appeared to lie in the same horizontal plane as the robot handle. The coordinate system of the touch screen and

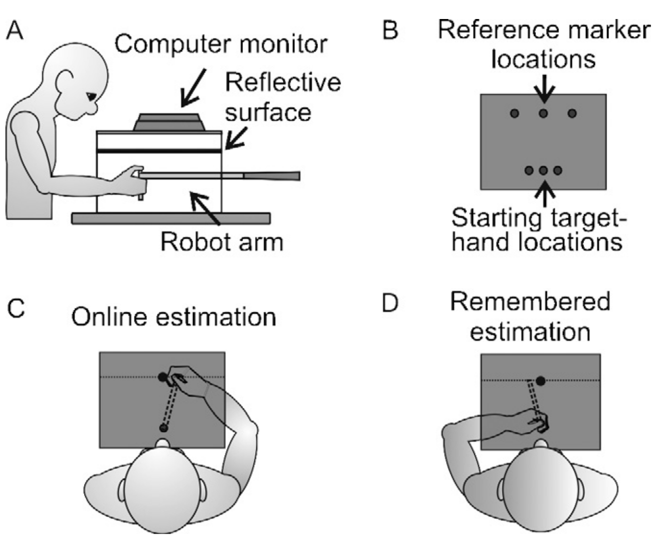

Fig. 2. (A) A side view of the experimental set up used in our proprioceptive estimation tasks. Participants gripped the handle of a robot manipulandum with an unseen hand-target (in this example schematic the right hand-target). A computer monitor projected visual references onto a reflective surface above the robot handle. Participants indicated if their unseen hand was to the left or right of the visual reference on each trial. (B) Starting positions of the hand-target and visual reference locations. On each trial, participants indicated if the final position of the hand-target was to the left or right of a visual reference. (C) In the online estimation task, participants indicated if the felt position of the hand-target was to the left or right of the visual reference (solid black dot). (D) In the remembered estimation task participants indicated if the remembered position of the hand-target had been to the left or right of the visual reference (solid black dot).

the robot manipulandum were aligned so as to permit a comparison of actual and perceived hand-target position.

Participants completed two proprioceptive estimation tasks with both the left and right hand-targets (four separate one hour sessions): online (Fig. 2C) and remembered estimation (Fig. 2D). The hand-target began in one of the three start locations (Fig. 2B). In both estimation tasks, on 50% of the trials when the hand-target began in the center start location, the hand-target was represented using a green cursor (same as the lit trials in the reach and reproduction tasks). Once this cursor disappeared or following one second (for un-lit trials), participants were prompted to actively move the hand-target along a constrained path created by the robot manipulandum to a location to the left or right of one of the three visual references (visual reference locations were the same as the target locations used in the reach and reproduction tasks, shown in Fig. 2B). In the online estimation condition, when the hand-target reached this location (Fig. 2C), the visual reference (a yellow circle) appeared (shown as the solid black dot in Fig. 2C). Participants then indicated, using the arrow keys on a keyboard, if the felt position of the hand-target was to the left or right of the visual reference. The hand-target was actively returned to the next randomly selected start position (guided along a constrained path by the robot manipulandum) where the next trial began. The method was the same in the remembered estimation paradigm, except that the hand-target was actively returned to a randomly selected start location *prior* to the appearance of the visual reference (Fig. 2D). On each trial participants were instructed to indicate if the remembered location of the unseen hand-target had been to the left or right of the visual reference.

In order to determine the location at which participants felt their hand was aligned with a visual reference, we adjusted the location of the hand-target with respect to each visual reference over trials using a two-alternative forced choice (2-AFC) adaptive staircase algorithm (Cressman & Henriques, 2009, 2010; Jones et al., 2010). For each start location (treating the center and center lit (hand-target represented by a cursor) start locations separately) and reference marker combination there were two corresponding staircases, a left and right, which were adjusted independently and randomly interleaved (24 staircases in total). Each staircase began such that the hand-target was 3 cm to the left or right of a given visual reference. The position of the hand-target was then adjusted over trials depending on the subject's response history. Approximately 25 judgments were made for each of the 24 staircases resulting in 600 trials. If subjects associated a specific felt location of the hand-target with a given reference marker, the two staircases (for a given visual reference and condition) converged toward a certain position at which subjects had an equal probability of reporting that the hand-target was to the left or right of the visual reference. This position will be termed *bias*.

As the bias indicates the position at which participants feel their hand is aligned with a particular reference marker, a leftward bias indicates that participants feel that their hand is more *rightward* than its actual location and a rightward bias indicates that participants feel their hand is more *leftward* than its actual location. To better compare these biases with horizontal errors observed in our reach and reproduction tasks, we flipped the biases so that a leftward bias or a rightward bias would indicate the same misestimate of hand position as a leftward or rightward horizontal error, respectively, in our reach and reproduction tasks.

As a measure of precision in our estimation tasks, an *uncertainty range* around the bias location was calculated. The uncertainty range is the difference between locations where participants responded that their hand-target was 84% left and 84% right, encompassing the center 68% of the distribution. The range between an 84% point (either left or right) and the 50% bias point is equivalent to one standard deviation (as measured in the reach and reproduction tasks). Thus, we use half of the uncertainty range (which we will also call the uncertainty range) when we compare the precision of localization in the estimation task with the horizontal standard deviation of reach endpoints and reproductions in the reach and reproduction tasks. Biases and uncertainty values related to a particular reference marker were excluded if the associated uncertainty was greater than mean uncertainty across all reference markers within the experiment plus two standard deviations (Jones et al., 2010). In total 15 trials (or <1%) of hand-reference marker estimates were excluded.

6. Data analysis

Both accuracy and variability between hand-targets and among conditions (68% error ellipse area for our reach and reproduction tasks and half of the uncertainty range for our estimation tasks) was examined using a 2 (target hand: left, right) × 3 (starting target hand location: left, center, right) × 3 (final hand-target location: left, center, right) × 5 (task type: online reach, remembered reach, reproduction, online estimation, remembered estimation) repeated measures ANOVA. As starting and final hand-target location were varied in the horizontal direction and only horizontal estimates of hand position were obtained in the estimation tasks, we assessed the effects of these variables on horizontal errors. Starting and final hand-target locations were included in the RM ANOVA as two separate variables. As such, the interaction between these two variables reflects the effect of hand-target movement path on proprioceptive localization. All ANOVA results are reported with Greenhouse-Geisser-corrected *p* values. Bonferroni correction was used to control for multiple comparisons.

As the orientation of the scatter of reach endpoints (i.e. the orientation of the 68% error ellipses) are in angle form, circular statistics was used to compare the pattern of reach endpoint scatter (i.e. orientation of the major axis of the elliptic fit) across conditions, hand-targets, and start and final hand-target locations. The "circular" package (Jammalamadaka & SenGupta, 2001) in R (version 2.10.0) was used to test our ellipse orientation circular data. Significant Watson's goodness of fit tests indicated that von Misesness, a circular analogue of linear normality, was violated, in all conditions, for both hand-targets, and all start and target locations (all $p < 0.05$). The ellipse orientation values did not lie tightly around the mean, were non-symmetrical and included some clustering at the two extremes, so they cannot be approximately treated as linear data. As such, Watson two-sample tests of homogeneity of the distributions for circular data were used to compare ellipse orientations among the reach and reproduction conditions, hand-targets, start and final hand-target positions. The Watson two-sample test is the non-parametric circular analogue to the Mann–Whitney *U* test for linear data (Mardia & Jupp, 2000). Mu (μ) and kappa (κ) were used as indices of the differences found among these distributions. A value of μ that approaches zero indicates more vertical ellipse orientations and higher magnitude values of μ indicate more horizontal ellipse orientations. An approximation to Bonferroni correction was applied to control for the number of Watson two-sample tests completed.

7. Results

We examined the effect of task goal, localization from memory, hand-target and movement path of the hand-target on the accuracy (signed and absolute horizontal errors) and precision with which participants could localize both the left and right hand-targets. We begin by describing the effect of task goal on *participants* overall accuracy and precision across the reach, reproduction and estimation tasks. Overall, we found that reaches were more precise when participants could see the hand-target in the start location (lit trials) than when the hand was not visible in this position (un-lit trials). However, reproduction and estimation precision did not differ across lit and un-lit trials, and whether the hand-target was lit in the center start location did not interact with any other task parameters, regardless of task. As such, we present data for un-lit trials only, for all tasks. A summary of the effects of task goal, proprioceptive memory, hand-target, and hand-target movement path on absolute and signed horizontal errors and precision are presented in Table 1. Significant effects are in bold.

7.1. Task goal

7.1.1. Reach and reproduction

Fig. 3 shows mean absolute (A) and signed (B) horizontal errors for each task and each hand-target (left hand-target: black bars and right hand-target: gray bars) for un-lit trials. In general, we found that participants were relatively accurate and precise when localizing an unseen hand-target with an average absolute horizontal error of 2.44 cm (SD = 1.92 cm) across reach tasks and 1.29 cm (SD = 1.02 cm) in the reproduction task (Fig. 3A). However, regardless of hand-target, absolute horizontal errors were larger in the two reach tasks (online: M = 2.40 cm and remembered: M = 2.48 cm) than in the reproduction task (reproduction: M = 1.29 cm; $F(2,18)$ = 39.39, $p < 0.05$). No differences in signed

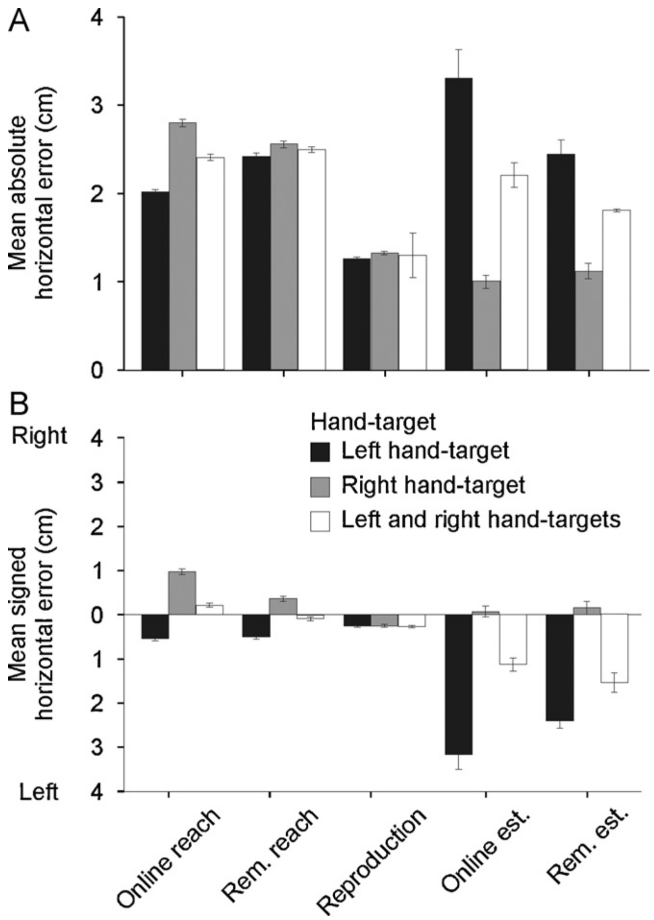

Fig. 3. Average absolute (A) and signed (B) horizontal error for each hand target (left: black and right: gray) and the mean across hand targets (white bars) in each task. Error bars are standard error of the mean.

horizontal errors were found among the reach and reproduction tasks ($F(2,18) = 1.45$, $p = 0.26$, Fig. 3B).

Reach and reproduction precision, as indicated by the size of 68% error ellipses, broken down by task goal (reach: A and B and reproduction: C), starting target hand location (left: blue, center: red, and right: green) and target location (ellipse position), are presented in Fig. 4, for un-lit trials. Observed differences in precision among the reach and reproduction tasks are discussed below in Section 7.2.

7.1.2. Estimation, reach and reproduction

Once again, participants were fairly accurate and precise across estimation tasks, especially for the right hand-target (gray bars in Fig. 3A and B); the average absolute and signed horizontal errors in the estimation task were 1.90 cm and 1.33 cm left, respectively (*average uncertainty range* = 1.71 cm). Overall, signed horizontal errors were larger and more leftward in the estimation tasks (1.75 cm left and 1.41 cm left, Fig. 3A and B) than those in the reach (0.55 cm right and 0.03 cm left; $F(3,27) = 10.87$, $p < 0.05$) and reproduction tasks (0.23 cm left; $F(2,18) = 9.01$, $p < 0.05$, Table 1). However, as evidenced by the black bars for the online and remembered estimation tasks in Fig. 3B, this difference was due to left hand-target biases. No differences in absolute horizontal errors were found among the reach and estimation tasks overall (p range: 0.19–1.0), but absolute horizontal errors for the left hand-target were larger in the online estimation task ($M = 3.30$ cm) than in the reproduction task ($M = 1.26$ cm; $F(2,18) = 7.33$, $p < 0.05$, black bars in Fig. 3A).

Fig. 5 shows biases (black symbols) and precision (uncertainty ranges shown by the colored bars) of proprioceptive localizations in each of our online (A) and remembered (B) estimation tasks for un-lit trials (when the hand-target was not represented by a cursor in the start location). Precision did not differ among the estimation and reach tasks (p range: 0.21–1.0), but did differ between the remembered estimation and reproduction tasks (as discussed in Section 7.2).

7.2. Task goal and proprioceptive memory

7.2.1. Reach

There were no differences in the direction or magnitude of horizontal reach errors between the online and remembered reach tasks (signed: $F(1,9) < 1$, $p = 0.42$; absolute: $F(1,9) < 1$, $p = 0.40$; Fig. 3A and B). But, participants were significantly less precise when reaching to remembered hand-target location (remembered: 12.82 cm^2, larger ellipses in Fig. 4B), than when reaching to the online location of the target hand (online: 6.49 cm^2; $F(1,9) = 6.31$, $p < 0.05$, smaller ellipses in Fig. 4A).

7.2.2. Estimation

No differences in the direction or magnitude of horizontal errors (signed: $F(1,9) < 1$, $p = 0.43$; absolute: $F(1,9) < 1$, $p = 0.56$, Fig. 3A and B) or precision ($F(1,9) < 1$, $p = 0.67$, Fig. 5) were found between the online and remembered estimation tasks.

7.2.3. Reach, reproduction and estimation

Absolute horizontal errors were larger, overall, in the remembered reach ($M = 2.48$ cm) and estimation tasks ($M = 1.78$) than in the reproduction task ($M = 1.29$ cm, $F(2,18) = 15.28$, $p < 0.05$, Table 1). Signed horizontal errors were also larger and more leftward in the remembered estimation task ($M = 1.16$ cm left) than in the remembered reach task ($M = 0.07$ cm left, $F(1,9) = 6.39$, $p < 0.05$, regardless of hand-target) and reproduction task ($M = 0.25$ cm left; $F(1,9) = 8.45$, $p < 0.05$). Both of these differences appear to be due to large left hand-target biases in the estimation tasks. Variability was also larger in the remembered estimation task (*average uncertainty range* = 2.16 cm) than in both the remembered reach ($SD = 1.89$ cm) and reproduction tasks ($SD = 1.23$ cm; $F(2,18) = 12.19$, $p < 0.05$, Table 1).

Table 1
The effects of task goal, proprioceptive memory, target-hand and target-hand movement path on the accuracy (absolute and signed horizontal errors) and precision of proprioceptive localization.

Effect	Absolute horizontal errors	Signed horizontal errors	Precision
Task goal	**$F(4,36) = 13.59$, $p < 0.05$**	**$F(4,36) = 6.43$, $p < 0.05$**	**$F(4,36) = 8.14$, $p < 0.05$**
Proprioceptive memory	$F(1,9) < 1$, $p = 0.86$	$F(1,9) < 1$, $p = 0.69$	**$F(1,9) = 9.05$, $p < 0.05$**
Task goal × proprioceptive memory	**$F(2,18) = 15.28$, $p < 0.05$**	**$F(2,18) = 6.05$, $p < 0.05$**	$F(1,9) < 1$, $p = 0.42$
Hand-target	**$F(1,9) = 11.62$, $p < 0.05$**	**$F(1,9) = 32.93$, $p < 0.05$**	$F(1,9) < 1$, $p = 0.96$
Task goal × hand-target	**$F(4,36) = 10.14$, $p < 0.05$**	**$F(1,9) = 12.30$, $p < 0.05$**	$F(4,36) = 2.39$, $p = 0.14$
Hand-target movement path	$F(4,36) = 1.21$, $p = 0.42$	$F(4,36) < 1$, $p = 0.44$	$F(4,36) < 1$, $p = 0.66$
Task goal × hand-target movement path	**$F(16,144) = 5.19$, $p < 0.05$**	$F(16,144) = 1.04$, $p = 0.39$	$F(16,144) = 1.29$, $p = 0.29$

Significant effects are in bold.

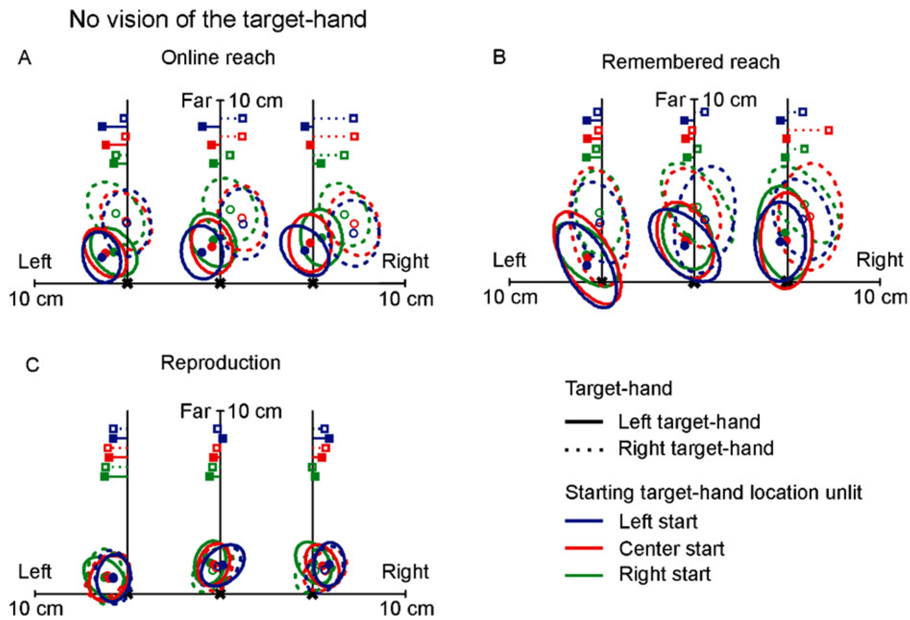

Fig. 4. Average errors (center of ellipses) and precision of reach endpoints (68% error ellipses) broken down by hand-target (left hand: solid ellipses and center circles, right hand: dotted ellipses and open center circles), start location (color: left start-dark blue, center start-red, right start-green) and target location (groups of ellipses) for the online reach (A), remembered reach (B) and reproduction (C) conditions when participants did not have vision of the hand-target in the starting position. The target positions are indicated by the solid black Xs. The magnitude and direction of horizontal error for each start and target position is emphasized by the solid (left hand-target) and open square (right hand-target) bars at the top of the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

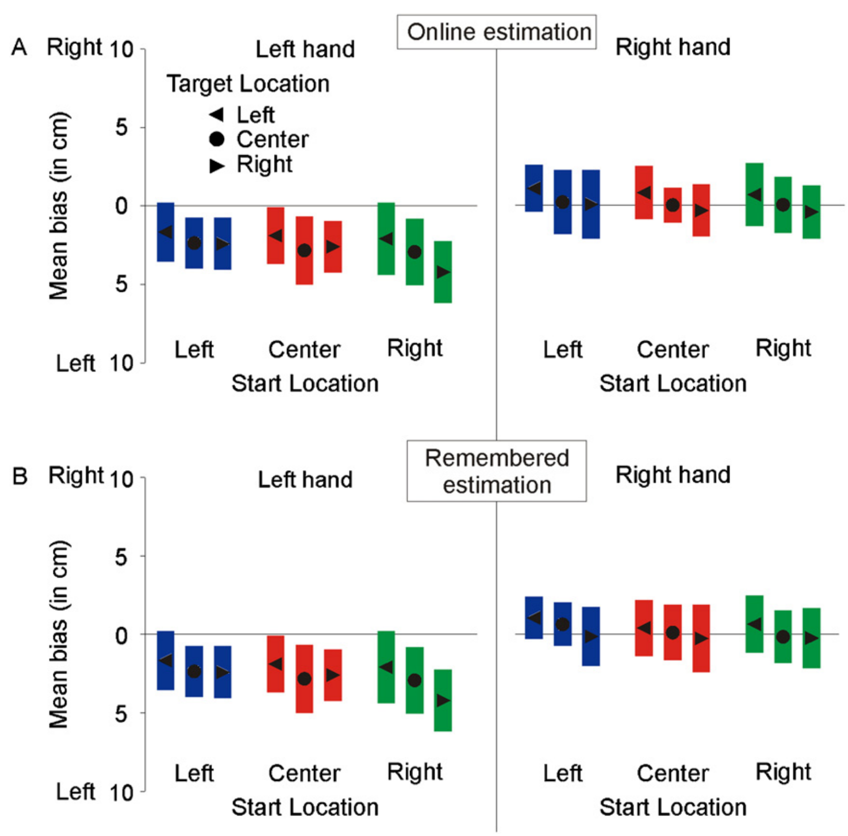

Fig. 5. Average biases (symbols in the center of bars) and precision (uncertainty range represented by the length of the bars) for the online estimation (A) and remembered estimation (B) paradigms for the left (left panels) and right hand-targets (right panels), broken down by starting (color: left start – dark blue bars, center start – red bars, right start – green bars), and final hand-target location (symbols: left target location – leftward pointing triangles, center target location – circles, right target location – rightward pointing triangles) when participants did not receive visual information about the starting position of the hand-target. The ends of each box are the locations where participants judged their hand-target to be left (bottom of the box) or right (top of the box) of the visual reference location 84% of the time. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

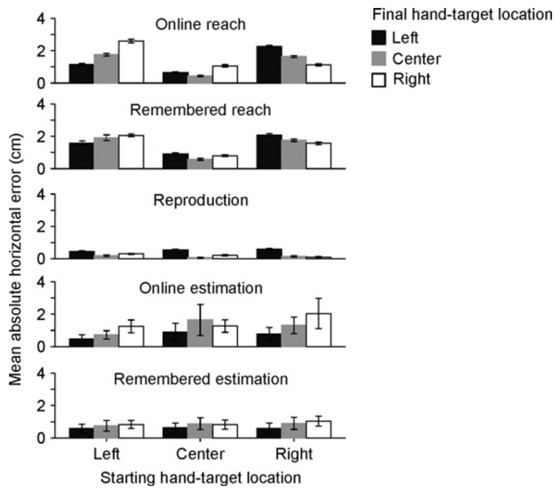

Fig. 6. Average absolute horizontal errors for each starting and final hand-target location pairing for each task. Error bars are standard error of the mean.

7.3. Task goal and hand-target

7.3.1. Reach

In the online and remembered reach tasks participants indicated that their left hand-target felt more leftward ($M = 0.49$ cm left, black bars in Fig. 3B) than their right hand-target ($M = 0.66$ cm right; $F(1,9) = 17.41$, $p < 0.05$, gray bars in Fig. 3B). Participants also made larger errors when reaching to the right target hand ($M = 2.63$ cm) than the left target hand ($M = 1.86$ cm) in the active reach condition (Fig. 3A; $F(1,9) = 14.53$, $p < 0.05$); no difference was found in the magnitude of reach errors across the two hands in the remembered reach condition ($p = 0.55$). There were also no differences in reach precision (68% error ellipse area) across the two hand-targets (LH: 7.82 cm^2 and RH: 9.54 cm^2, $F(1,8) = 3.29$, $p = 0.10$), for both online and memory-guided reaches ($F(1,8) = 0.10$, $p = 0.75$).

7.3.2. Reproduction

Neither absolute (Fig. 3A) nor signed horizontal errors (Fig. 3B) varied across hand-targets in the reproduction condition ($F(1,9) < 1$, $p = 0.60$ and $F(1,9) < 1$, $p = 0.98$, respectively). There were also no differences in reproduction precision across the hand-targets (LH: and RH: $F(1,9) = 0.53$, $p = 0.49$, solid and dotted ellipses in Fig. 4C).

7.3.3. Estimation

In our estimation tasks (Figs. 3 and 5), participants once again misestimated the felt position of both hand-targets (signed horizontal error). Overall, regardless of the estimation task ($F(1,9) < 1$, $p = 0.86$), participants judged their left hand-target to be more leftward ($M = 2.93$ cm left, black bars in Fig. 3B and left panels in Fig. 5) and their right hand-target to be more rightward ($M = 0.11$ cm right, gray bars in Fig. 3B and right panels in Fig. 5). Participants also made larger estimation errors when estimating left hand-target position (online: $M = 2.76$ cm; remembered: $M = 2.59$ cm) than right hand-target position (online: $M = 1.24$ cm; remembered: $M = 1.19$ cm). But, as seen in Fig. 5, participants were equally precise across the two hands (Left: *average uncertainty range* (*average SD*) = 1.14 cm, Right: *average SD* = 1.08, $F(1,9) = 0.58$, $p = 0.46$), regardless of whether estimates were based on online or remembered hand position ($F(1,9) = 1.77$, $p = 0.21$).

7.4. Task goal and hand-target movement path

Fig. 6 shows absolute horizontal errors for each starting and final hand-target location pairing for each task. Overall, hand-target movement path (as measured by the interaction between starting and final hand-target positions) did not affect absolute or signed horizontal errors ($F(4,36) = 1.21$, $p = 0.42$ and $F(4,36) < 1$, $p = 0.44$, respectively, Table 1). However, the effect of hand-target movement path interacted with task goal (Table 1). Specifically, hand target movement path affected absolute horizontal errors in the online reach task only; errors were largest for left hand-target positions (black bars in Fig. 6) when paired with the right starting hand-target location and for right hand-target locations (white bars in Fig. 6) when paired with the left starting hand-target location.

8. Discussion

We sought to systematically compare proprioceptive localization of the left and right hand-targets using three methods, within the same experimental environment, with the same participants and task parameters. We compared performance in a perceptual estimation task in which participants indicated the felt position of a hand-target relative to visual references (no goal directed movement), and in two goal-directed movement tasks typically used to assess proprioceptive localization, reaching and reproduction. This comparison allowed us to determine if previously observed differences in proprioceptive localization are because of true variations in the proprioceptive position sense or variations in the goal of the task, and whether this further depends on the hand being tested/localized. That is, the initial coding of proprioceptive target location may be similar across tasks, but the way or the purpose for which the information is used could elicit differences in accuracy and precision. Although we found that participants were fairly accurate and precise when localizing a hand-target, we also found variations in the accuracy and precision of proprioceptive localizations across tasks and task parameters that may reflect differences in the way the brain codes and uses proprioceptive information about target location. We will first provide an overview of the results and then discuss how task goal, localization from memory, hand-target and movement path affected localizations across our tasks.

Overall, while the magnitude of localization errors was greatest in the estimation task (particularly for the left-target hand), participants were less precise when reaching to or reproducing hand-target location than when estimating hand-target location. Localization from memory had the greatest effect on reaches; participants were less precise when reaching to the remembered location of the hand-target than when reaching to its online location. There was no change in precision between the online and remembered estimation tasks. Across all reaching and estimation tasks, participants perceived their left hand-target to be more leftward and their right hand-target to be more rightward than their actual positions. This hand-target effect was not found in the reproduction task. Movement path of the hand-target does not appear to affect localization in these tasks. Overall, the differential effects of localization from memory and hand-target suggests that either the types of sensory information used by the CNS to localize a proprioceptive target depends on the eventual goal of localization or that the way this sensory information is processed may differ across task goals.

8.1. Task goal

Much like what has been found for vision (Goodale & Milner, 1992), research has suggested that proprioceptive information is processed differently depending on its functional use (e.g. action versus perception) (Dijkerman & de Haan, 2007). We compared performance in tasks in which the goal involved planning a movement to a designated location to a task in which the judgement of hand-target position was made relative to visual references. We not only found variations in accuracy and precision of proprioceptive localization across tasks in general, but we also found a differential effect of localization from memory and hand-target on the accuracy and precision of proprioceptive localization across task goals. This will be the focus of the following two sections.

8.2. Task goal and proprioceptive memory

Participants were much less precise when reaching to the opposite hand from memory than when reaching to its online location. Chapman et al. (2001) also reported a decrease in precision when participants reached to the remembered location of an unseen hand, an effect these authors attributed to a decay in the memory trace of the proprioceptive target. However, we also found that proprioceptive localization from memory had a greater effect on reaches than estimations. In fact, there were no differences in the accuracy and precision of estimations between the online and remembered tasks. This differential effect of memory across reach and estimation tasks could be due to the complexity of the task – for example, maintaining a motor plan in memory may be more difficult or employ different neural networks than simply remembering the spatial location of a hand (e.g. Curtis, Rao, & D'Esposito, 1994). This study is among the first (e.g. Jones et al., 2010) to compare remembered proprioceptive localization ability across different task goals.

8.3. Task goal and hand-target

For both online and memory-guided reaching, horizontal errors were more leftward when the left hand was the target and more rightward when the right hand was the target, but were similar in magnitude. This pattern of hand-target bias is consistent with those reported in proprioceptively guided reaching (Crowe, Keessen, Kuus, van Vliet, & Zegeling, 1987; Haggard, Newman, Blundell, & Andrew, 2000; Jones et al., 2010; van Beers et al., 1998) and saccade tasks (Ren & Crawford, 2009), in which reaches or saccades made to the right hand-target are deviated more rightward and reaches or saccades made to the left hand-target are deviated more leftward. Here, we also found the same pattern of bias in our estimation tasks. And previous research in our lab found similar lateral mis-estimations of final hand-target location for a larger number of targets (Jones et al., 2010), and even for proprioceptive estimates of hand position following visually guided reach training to visual targets with the same hand (Salomonczyk, Henriques, & Cressman, 2010). Wilson et al. (2010) also reported leftward biases for the left hand-target and rightward biases for the right hand-target when participants compared hand-target location to remembered proprioceptive or visual references (left or right or forward or backward relative to the references). This similar hand-target effect, across reach, saccade and perceptual tasks, suggests that this pattern is independent of the motor system, or the overall goal in which proprioception is being used. In fact, these hand-dependent effects could reflect priors associated with the location of the hand-targets themselves and where we tend to use them in space – the left hand tends to remain more on the left of our body and the right hand tends to remain to the right. Thus, the leftward and rightward sides of space are the most likely locations of the left and right hands, respectively.

However, we did not find any differences between the left and right hand-targets in our reproduction task. Similar results were reported by Goble and Brown (2007, 2008) and Goble et al. (2009) who also did not find any differences in accuracy between left and right hand/arm targets when participants reproduced arm position using the same arm, although they did find a left arm accuracy advantage for proprioception in contralateral matching tasks (Goble & Brown, 2007, 2008; Goble et al., 2009) which is more analogous to our reaching tasks. Hand-target dependent differences between reach, estimation and reproduction tasks may, therefore, be due to the way in which the proprioceptive information about the hand-target is used, and transmitted within the brain. Reaching to a proprioceptive target with the opposite hand (or even the eyes) likely requires additional computations (e.g. the computations involved in interhemispheric transfer of relevant proprioceptive and motor information) than reproducing location with the same hand. These results suggest that matching or reaching with the opposite arm is more difficult, and thus may be able to elicit dominant/non-dominant arm accuracy advantages. Likewise, comparing the location of the proprioceptive target with respect to either visual reference markers (in this study and our previous study, Jones et al., 2010) or with respect to a proprioceptive reference, like body midline, the other hand, or a remembered hand-target location (Fiehler, Rösler, & Henriques, 2010; Jones et al., 2010; Wilson et al., 2010) likely also involve additional computations or transformations. These might include the computations needed to maintain the proprioceptive reference in memory or the transformations among reference frames that allow the reference marker and hand-target to be compared. However, the fact that there are no differences between judging the unseen hand relative to a visual reference or a proprioceptive reference (Cressman & Henriques, 2009; Fiehler et al., 2010; Jones et al., 2010; Wilson et al., 2010) suggests a modality-independent mechanism of spatial location (at least for visual and proprioceptive information).

8.4. Task goal and hand-target movement path

We examined if how the *proprioceptive target* arrives at a target position or the movement path of the hand-target affected proprioceptive localization of that hand-target. Although previous research has shown that both starting and final hand-target location affects localization we did not find that the movement path of the hand-target affected localization in our remembered reach, online and remembered estimation or reproduction tasks. In contrast, in our online reach task, we found a partial interaction between starting and final hand-target location on absolute horizontal reach errors such that errors were largest for the left final-right start and right final-left start location pairings. However, there was no effect of hand-target movement path on signed horizontal reach errors or reaching precision in this task.

The non-effect of hand-target movement path suggests one of two possibilities – either the CNS is not using the dynamic signals about hand-target movement to localize the hand-target in its final location (i.e. so the path of the target is merely ignored) or this information is being used extremely accurately in these tasks. For example, we used relatively small separations between starting (2.5 cm) and final hand-target locations (5 cm) which may not have been large enough to reveal possible movement path dependencies when localizing the hand in its final location. Additionally, previous work in our lab also found no differences in proprioceptive localization between active and passive movement of the hand-target (Jones et al., 2010), nor differences in the effects of hand-target movement path across active and passive movement conditions (Kappers et al., 2010). Further research using larger separations, across a larger area of space, is needed to better examine the effect of hand-target movement path on localization of that target in its final position. This is the first study that we know of to examine how the movement path of the proprioceptive target affects proprioceptive localization; and particularly across different task goals.

9. Summary and practical significance

The present study provides an extensive exploration of the accuracy and precision of proprioceptive localization for both the left and right hands under a variety of conditions. Overall, localization seems poorer, and more influenced by task parameters, when proprioception is used to guide a reach with the opposite hand, particularly from memory, and best when merely reproducing the proprioceptive target site.

Overall, our findings suggest two possible variations in the way the CNS processes sensory information across tasks: (1) the way the CNS processes proprioceptive information about hand-target location differs depending on the task goal (e.g. action versus perception); (2) the sources of sensory information used by the CNS, for example those provided by task parameters, may vary with the task goal. These findings could have eventual practical applications within the assessment of sensory deficits and the effectiveness of neuro-rehabilitation following injury or disease. For example, if participants' proprioceptive localization ability varies with the task goal, then it follows that special care must be taken to select the task that most accurately assesses deficits in this ability. Further, if different tasks elicit different processing responses in the CNS, then it follows that one task may not be sufficient for re-establishing failing or lost neuronal connections. Further research is needed to examine how these different proprioceptive localization tasks affect the outcomes of rehabilitation.

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