Proprioceptive Localization of the Fingers: Coarse, Biased, and Context-Sensitive

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Abstract—The proprioceptive sense provides somatosensory information about positions of parts of the body, information that is essential for guiding behavior and monitoring the body. Few studies have investigated the perceptual localization of individual fingers, despite their importance for tactile exploration and fine manipulation. We present two experiments assessing the performance of proprioceptive localization of multiple fingers, either alone or in combination with visual cues. In the first experiment, we used a virtual reality paradigm to assess localization of multiple fingers. Surprisingly, the errors averaged 3.7 cm per digit, which represents a significant fraction of the range of motion of any finger. Both random and systematic errors were large. The latter included participant-specific biases and participant-independent distortions that evoked similar observations from prior studies of perceptual representations of hand shape. In a second experiment, we introduced visual cues about positions of nearby fingers, and observed that this contextual information could greatly decrease localization errors. The results suggest that only coarse proprioceptive information is available through somatosensation, and that finer information may not be necessary for fine motor behavior. These findings may help elucidate human hand function, and inform new applications to the design of human-computer interfaces or interactions in virtual reality.

Index Terms—Proprioception, Localization, Multisensory integration

1 Introduction

The proprioceptive sense provides us with information about the posture of our body. Sensory afferent nerves terminating in muscles spindles, joints and skin convey information about the configuration of the limbs and other body parts to the central nervous system (CNS) [1]. This information is also combined with input from vision and other sources [2], aiding sensorimotor coordination, and helping to maintain a body schema, an internal brain representation about how the body is positioned. This information is also instrumental to the planning of motor tasks [3], the perception of our body and the state of the environment around us.

The brain demonstrates considerable flexibility in integrating multisensory information about the body. Prior research indicates that it can take ownership of a wide variety of hand representations [4], an idea that is particularly relevant for first-person virtual reality simulations that represent the hands and fingers. When immersed in virtual reality, users have been reported to experience greater agency over simpler hand representations. This has been attributed, in part, to the brain's sensitivity to position errors in the display of virtual limbs [4]. However, there is little direct evidence about how limb positions are perceived in the presence of visual-proprioceptive mismatches. Because visual and proprioceptive information is integrated in forming estimates of the position of parts of the body [3], [5], [6], it could be deduced that such mismatches might decrease immersion. To date, however, it is unknown how accurately the locations of each of the fingers can be perceived without the use of vision.

Several studies have explored proprioception for the arm by examining the errors that manifest when the arm points to a displayed visual target [7], to a prior location of the hand [8], or to the perceived location of the unseen other hand [9]. All studies reveal large errors in arm localization, in the order of several centimeters. Further studies that have examined proprioceptive errors for various types of visuo-haptic matching tasks show that the observed errors generalize across various experimental designs [10]. Proprioceptive accuracy is improved if the muscles of the arm are actively engaged in movement [11], which has been interpreted to imply that efferent signals, which command the muscles to move, can enhance proprioceptive performance. Cutaneous manipulations, including skin stretch, have also been shown to influence proprioceptive localization of the limb [12]. Proprioceptive reaching has been shown to utilize both body and gaze-centered reference frames [13]. The proprioceptive map appears to be both idiosyncratic, varying from person to person, and stable, changing little over time [8], [14]. Proprioceptive localization errors for the hands (i.e., limb position) exhibit systematic differences [15], [16], and the errors vary with the posture of the limb [16]. However, it is unknown if these results generalize to the localization of the fingers. None of these studies have characterized the proprioceptive localization of individual fingers. Consequently, other potentially salient factors, such as effects of hand pose on proprioceptive errors in finger

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localization, have not been previously explored. The fingers are of particular interest because of their important role in performing fine motor tasks, and proprioceptive information in particular has been shown to be utilized in computing joint-based motor commands [17].

In order to characterize multi-digit proprioceptive localization, we designed a study in which subjects reported the perceived positions of their fingertips without visual feedback, using a virtual reality (VR) environment and multipoint tracking system. Several techniques could be used to assess multi-digit proprioception – for example, by asking subjects to evaluate the postural similarity between a virtual hand and their own, or by asking them to judge when the two differed. Here, we assessed proprioceptive localization using a method that is similar to those used in prior studies of limb proprioception [16]. In it, subjects had their hand placed on a table and selected the perceived location of an unseen digit or digits, by guiding a visual cursor to the perceived location in a VR environment that was carefully calibrated to match the real environment. This method was chosen because of its time efficiency, because it provides a direct report of the location of each finger, and because it allowed us to exclude other potential confounds, such as motor or perceptual errors from the contralateral hand. The use of the VR system provided flexibility in the design of experimental tasks, as evidenced by Experiment 2 below.

In addition to the somatosensory proprioceptive sense, vision also plays an important role in providing information about the body position. Various studies have also explored the integration of visual and proprioceptive cues in the formation of whole limb position percepts [5], [18], or in motion planning and reaching [19], [20], [21], and such studies have informed models for the integration of visual and proprioceptive information [5]. Studies on the rubber hand illusion [22], [23] have also shown that visual information in combination with other cues can cause an adaptation of proprioceptive estimates.

In our daily lives, we routinely encounter situations in which multiple senses are combined. Frequently, this occurs in contexts in which incomplete sensory information is available. For example, a body part may be occluded from view (by the body or another object in the environment), while visual feedback of the adjoining body segments is still available. This is commonly observed in the hand, due to occlusion of the fingers in many practical tasks. Prior literature has provided limited insight into how visual context, in the form of visual cues as to the location of adjacent body parts, affects localization of a visually occluded part, especially for the fingers. In order to assess the influence of this indirect visual information on proprioceptive localization of the fingers, we designed a second study in which we measured how subjects' ability to localize their fingertips was affected by visual feedback about locations of the other fingers.

In the sections that follow, we present a first experiment on the proprioceptive localization of multiple fingers, and a second experiment in which we assess the effect of visual context on proprioceptive localization, in the form of visual cues as to the locations of adjacent fingers. We discuss the findings and their implications for understanding human haptic function, and point toward open questions and potential applications.

2 Experiment 1 : Proprioceptive Localization of Fingers

2.1 Methods

2.1.1 Subjects

Twelve subjects (8 male; 23 to 33 years of age) volunteered in this experiment. All subjects were naive to the purpose of the experiment. All subjects had (corrected-to-) normal vision, and gave their written informed consent. Two subjects self reported both hands to be dominant, while the rest reported their right hand as the dominant hand. The experiment was approved by the human subjects research review board of the University of California, Santa Barbara.

2.1.2 Apparatus

The experimental apparatus consisted of a computer, virtual reality headset, and multipoint tracking system (Fig. 1). Subjects were seated in front of a table and wore a stereoscopic head mounted display (HMD) (Rift, Oculus VR Inc, Menlo Park, CA). The HMD provides stable tracking of the headset in 3D space, accurate to within a millimeter. The HMD displayed a calibrated version of the table in its virtual environment. A careful calibration of the real and virtual environment was performed, by using sensors to select multiple points on corresponding objects with identical dimensions and locations in the real and virtual spaces, and implementing an affine transformation that superimposed the two. This ensured accurate dimensions and placement to within 2 mm. Ground truth positions of the fingers were obtained through six degree-of-freedom wired electromagnetic sensors for position and orientation (Micro Sensor 1.8 and Liberty tracker, Polhemus Inc., Colchester, VT) that were worn on all five fingers and wrist of the left hand, and that were sampled at a frequency of 240 Hz. These sensors tracked finger and wrist locations with sub-millimeter accuracy and without data loss or occlusion. The sensors were attached by means of custom brackets and double sided prosthetic tape. Slim, custom brackets were designed and selected to fit the fingernails of each subject and positioned relative to standard anatomical features. Although forces due to the sensors were low, the attachment of sensors to the fingernails via these brackets mitigated cutaneous cues that might otherwise influence proprioceptive judgments [12].

A video projector displayed target positions at computer-specified locations on the table surface, enabling the experimenter to position the subject's hand in each required posture (see Procedure). A wrist rest was fabricated and attached to the table for subjects to place their wrist on during the experiment. A detent in the wrist rest interlocked with a conical bit affixed to the wrist ensuring consistent placement between trials. In all but one of the test conditions, the wrist rest was displayed (at its corresponding location) in the virtual environment. Thus, both visual and cutaneous information about the location of the wrist was available to subjects during the experiment. Visual instructions were provided to subjects via the virtual environment, and a computer mouse enabled them to select perceived fingertip locations.

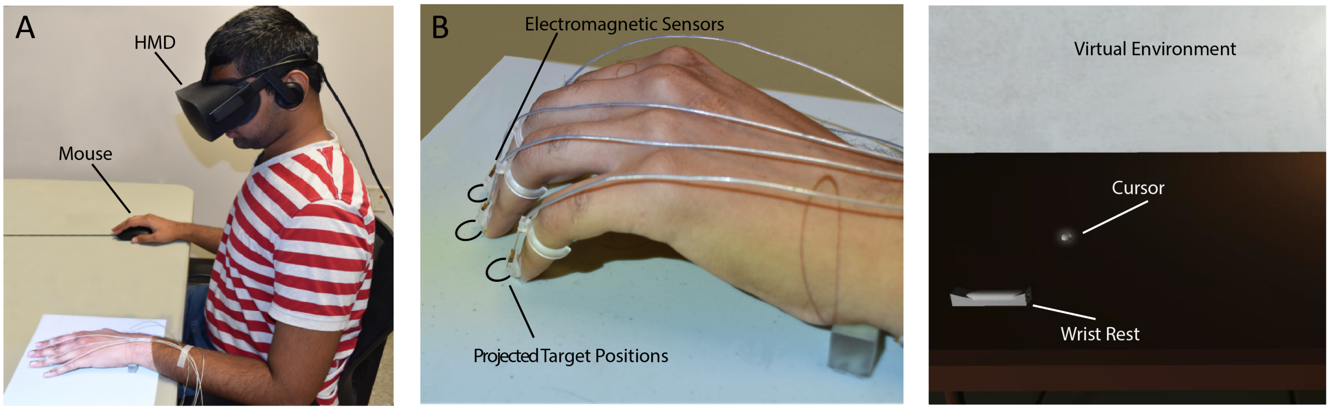

Fig. 1. A) Experimental System. The subjects left hand was moved to specific hand poses displayed on the table. Subjects used the computer mouse to report perceived positions of their fingertips in the calibrated virtual environment. B) Left hand, showing sensors attached holding a hand pose. C) Displayed Virtual Environment.

2.1.3 Target hand poses

Participants hands were positioned in one of five distinct hand poses (P1 to P5; Fig. 2), so that we could examine the dependence of proprioceptive errors on finger locations. These poses included a "relaxed" pose (P1), a pose in which all fingers were flexed (P4), and other combinations of flexed and extended fingers. In pose P5, the thumb was flexed inward, towards the palm. The visual display of the wrist rest was included for all these conditions. To examine effects of visual feedback about the wrist position on perceived fingertip location, we repeated pose P1 while omitting the visual display of the wrist rest (P1 without wrist display). Each pose was specified as a set of target positions on the table. These poses were chosen from a subset of possible hand poses constructed by considering two distinct locations for each finger and three distinct locations for the thumb. This choice of poses allowed us to efficiently study the effect of changing the position of the thumb (P1 vs. P5, P2 vs. P3), index finger (P1 vs. P2), and the other fingers (P3 vs. P4).

Prior to the start of the experiment, the length of the subject's hand, from the center of the wrist to the tip of the middle finger, was measured, and the target positions were scaled accordingly. This was done to ensure that subjects maintained similar hand shapes for each pose. In what follows, we refer to the thumb as digit 1, and the little finger as digit 5.

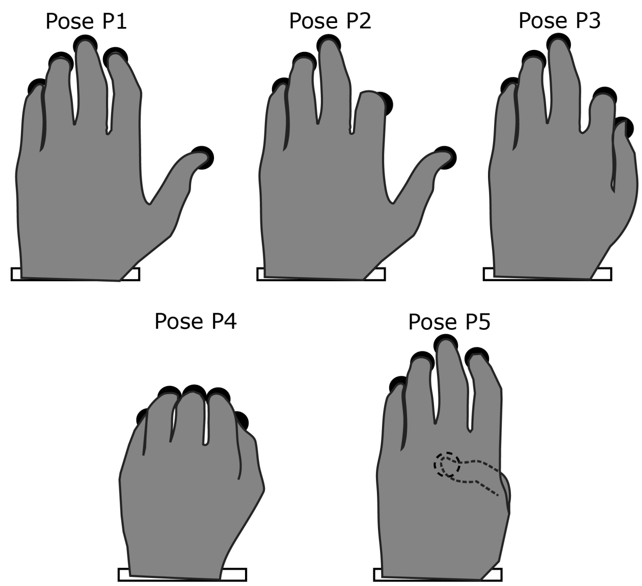

Fig. 2. Distinct target hand poses used in Experiment 1. P1: Natural resting pose, P2: Index finger flexed, P3: Thumb and index finger flexed, P4: All digits flexed, P5: Thumb flexed inwards. The black circles are the target positions for the fingertips. Dashed strokes are used to represent occluded sections. Note that none of the fingers were touching each other.

2.1.4 Procedure

At the beginning of the experiment, subjects experienced a familiarization phase, in which sensor data was used to animate a simple representation of the hand, with markers showing the precise locations of the fingertips. Subjects were encouraged to move their fingers and familiarize themselves with the virtual environment and the hand representation, and to convince themselves that it provided an accurate representation of the table in front of them. When subjects indicated they were acclimated, the experiment began. The hand was positioned with the wrist on the wrist rest, and the simple hand representation disappeared.

During each trial of the experiment, the experimenter moved the subject's fingers to the hand pose with specified target positions that were automatically projected onto the table, after which the subject held his or her hand at this location. The experimenter ensured that none of the subject's fingers were touching to limit the cutaneous cues available to the subject. The ground truth finger positions were recorded at this stage. The subject could then input a response. A cursor, in the form of a small sphere that was controlled by the mouse appeared at a randomized location. Subjects were prompted to use the mouse and cursor to select and click at the perceived location of each fingertip in sequence, from digit 1 (thumb) to digit 5 (little finger). The cursor was reset to a random location upon each click to prevent starting position bias. Once all positions were reported, a new hand pose was selected, and the next trial started.

Each of the six hand poses was repeated 15 times, for a total of 90 trials per subject. The poses were presented in block-randomized order, with each hand pose presented once within a random ordering, before moving to the next block of six hand poses. The experiment lasted 75 minutes on average for each subject.

2.1.5 Control Experiment

The hand could not be seen during the main experiment, in which participants wore the HMD displaying a virtual environment without any feedback about the positions of the fingers. Thus, the use of proprioception was required in order to report finger position. This reporting was performed within the virtual environment, so that the reported locations may be regarded as proprioceptive estimates in the body frame of reference, translated into the visual frame of reference [24].

In order to rule out the possibility that the measured errors in the primary experiment could be due to errors introduced by the HMD or the experimental design, such as sensor error, display distortion, input errors, scaling errors, object misalignment or other factors, we conducted a control experiment. We quantified errors in a condition in which participants could see their real hand location when reporting positions, by alternating between views of the real environment and calibrated virtual environment. Subjects accomplished this by raising and lowering the HMD until they were satisfied with the reported positions. Four subjects participated in the validation experiment, none of whom participated in the main experiment. Participants were asked to accurately align the cursor in the virtual environment with their fingers. By analyzing the reported finger locations, we determined that the magnitudes of the localization errors, as defined in the analysis below, were small, averaging 0.9 cm. This was strikingly lower than the errors reported in the main experiment, see below. There was no obvious pattern of bias to the resulting data. The errors were similar for all fingers. The error magnitudes obtained in this task were similar in magnitude to values that have been reported for visual estimation errors for nearby positions in virtual reality [25].

2.1.6 Analysis

The analysis of data from the main experiment compared the reported and veridical positions of the fingertips for each subject in each pose. The veridical and reported positions consisted of vectors in the two-dimensional plane of the surface, $\vec{p}^{\,v}_{i,f,s,t}$ and $\vec{p}^{\,r}_{i,f,s,t}$, respectively. Any errant input of a finger position, as self-reported by the subject during the trial (accounting for $< .5\%$ of all trials), was removed from the analysis. For each subject, finger, hand pose and trial (i, f, s, t respectively), we computed the error vectors $\vec{\varepsilon_i}$ between veridical and the reported positions.

$$\vec{\varepsilon}_{i,f,s,t} = \vec{p}^{\,r}_{i,f,s,t} - \vec{p}^{\,v}_{i,f,s,t} \tag{1}$$

The error vectors between the reported and ground truth positions were then translated to ensure that the veridical positions of each individual finger across the trials coincide, to account for any minor differences in the placement of the finger by the experimenter between trials. The errors were quantified by modelling the reported positions for each pose and finger with a bivariate normal distribution. Proprioceptive localization errors can include both systematic and random components. The magnitude of the displacement vector between the distribution mean and the true finger position is defined as $E_{i,f,s}$.

$$E_{i,f,s} = \Big| \frac{1}{N_t} \sum_t \vec{p}^{\,r}_{i,f,s,t} - \vec{p}^{\,v}_{i,f,s} \Big| \tag{2}$$

$E_{i,f,s}$, which is also the magnitude of the mean error vector, reflects the systematic error, or bias in the reported positions. The area of the 95% confidence ellipse, which is the smallest possible ellipse that would be expected to contain 95% of the locations in the distribution, reflects the random errors, or variability in the data [15], [16]. The same error measures were used for the validation experiment.

The magnitude of the mean error vector was averaged across the poses and compared with the mean errors obtained in the control experiment, using an independent-sample Student's t-test. The magnitude of mean error vector and the area of the confidence ellipse were compared between the discrete hand poses (P1 to P5) and digits via 5×5 repeated measures (RM) ANOVA tests. The normality of the data was evaluated using the Shapiro-Wilk test. Greenhouse-Geisser corrections were employed when sphericity was violated, and Bonferroni corrections were applied to the tests. By studying the effect of pose, it is possible to assess the effect of finger position on proprioceptive localization. In these analyses, we assumed that the reported positions for each finger are independent.

To compare the effect of visual information on the location of the wrist, we performed two 2×5 repeated measures ANOVA tests (Pose $\times$ Digit) on the magnitude of mean error vector and the confidence ellipse area data of poses P1 and P1 without wrist display, which differed only in the visual information that was provided about wrist location (via the displayed and felt wrist marker and wrist rest, and interlocking features).

The digit-wrist distance was computed as the distance between the tip of the digit and the center of the wrist, and we calculated the percentage differences between the reported and actual digit-wrist distances. The inter-digit distance was also computed for adjacent digits, and the reported distances were compared with the true distances.

2.2 Results

The reported positions and the confidence ellipses for all target positions for two subjects are shown in Fig. 3. The observed errors were large, averaging 3.7 cm (range 0.4 to 8.6 cm), and varied with the finger, pose and subject. The positions reported by six subjects for hand pose P1 are shown in Fig. 4. Results for a representative subject are shown in Fig. 5.

The errors observed in the primary experiment were significantly larger than those in the validation task ($p < 0.001$), at more than 400% as large. This suggests that the observed errors in the primary experiment were likely caused by proprioceptive sensing of finger locations. Thus, the contributions of distortions due to the display, input method, sensing apparatus, and virtual environment calibration likely played a smaller role.

The mean errors for each discrete pose averaged across all subjects are shown in Fig. 6. The results of the 5×5

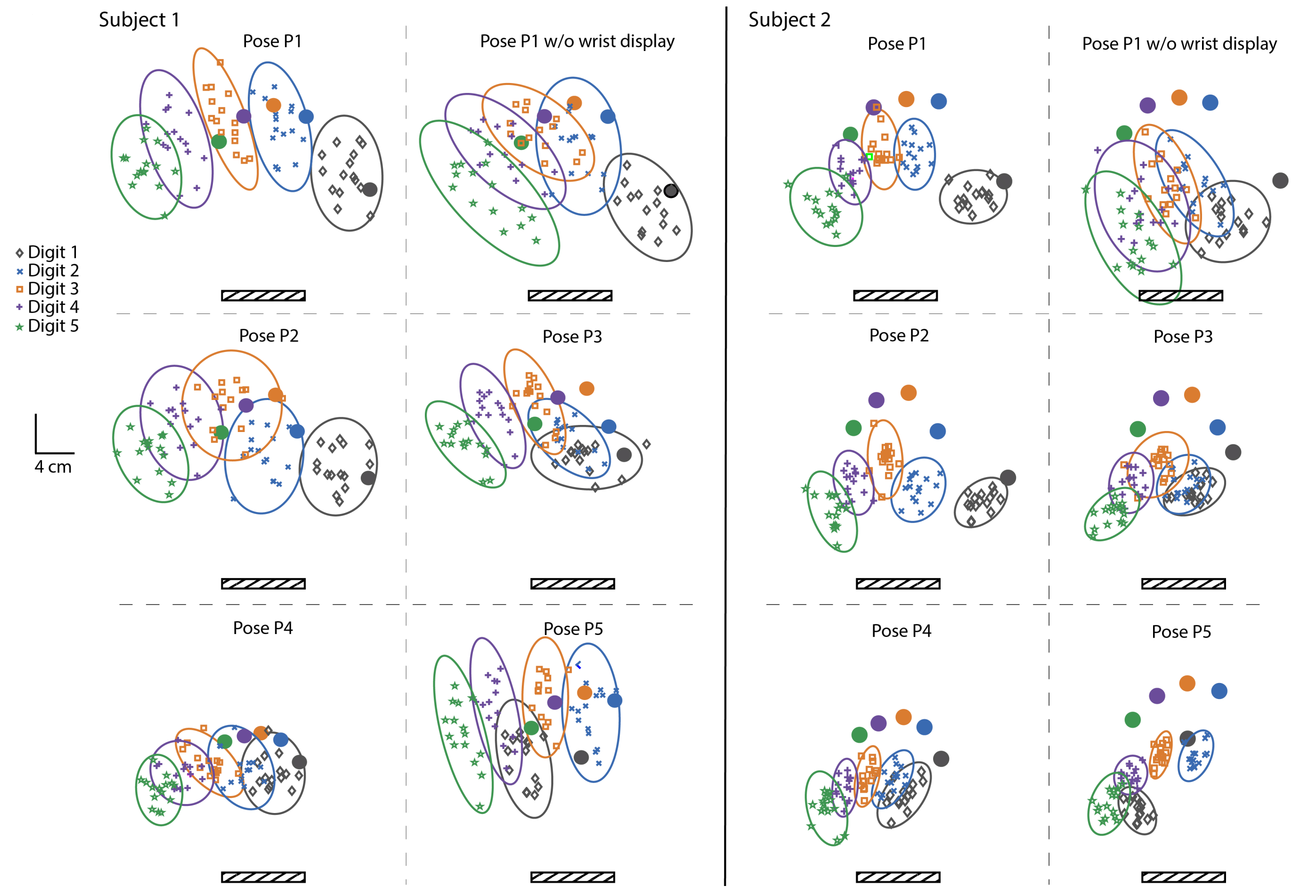

Fig. 3. Results for each hand pose for two subjects in Experiment 1. The solid circles represent the ground truth positions of each finger, and the hatched rectangle represents the location of the wrist. The reported locations for each individual digit over all trials are represented with a specific marker and color indicated in the legend. The ellipses are the 95% confidence ellipses for the distribution of each digit. The data shows a noticeable bias in the reported positions from the true position. The average error for Subject 1 across all fingers and poses was 4.17 cm (range 2.1-6.6 cm); the average area of the confidence ellipses was 39 cm^2 (range 17-72.4 cm^2). Results from subject 2 exhibited larger errors (mean 5.3 cm, range 2.5-7.8 cm), however localization is more precise than subject 1 (mean area of confidence ellipse 15 cm^2, range 3-50.6 cm^2). Results from subject 1 exhibited a consistent leftward bias in reported locations, whereas subject 2 reported the fingers to be more proximal to the wrist than the veridical positions.

(hand poses P1 - P5 $\times$ digits 1 - 5) repeated measures ANOVA on the errors showed a significant main effect of the digit ($F(1.321, 14.533) = 15.42, p = 0.001$). There was no significant effect of the pose ($p = 0.078$) and no significant interaction between the digit and pose ($p = 0.19$), which precludes within-factors analysis. The pairwise comparisons for digits showed that the errors of the thumb, index and middle fingers were significantly lower than those of the ring and little fingers. The errors of the middle finger were significantly higher from that of the index finger. There were no other significant comparisons (all p's > 0.125).

On comparing the errors for each digit averaged across all hand poses and subjects, we observed that localizations of digits 1 and 2 are generally most accurate (mean error 2.89 cm and 2.81 cm respectively) followed by that of digit 3 (mean error 3.66 cm), while localization of digits 4 and 5 were least accurate (mean error 4.4 cm and 4.7 cm respectively).

The 5×5 repeated measures ANOVA on the area of the confidence ellipse showed no significant effect of either pose ($p = 0.064$) or digit ($p = 0.14$). There was no significant interaction between the finger and pose ($p = 0.594$). Confidence ellipse areas were smallest for pose P4 (mean 29 cm^2), and largest for pose P1 (mean 43 cm^2). The area of the ellipse was smallest for digit 1 (mean 32 cm^2), and largest for digit 3 (mean 39 cm^2), but these results are not statistically significant.

The errors and areas of the confidence ellipse for poses P1 and P1 without wrist display are shown in Fig. 7. The results of the 2×5 repeated measures ANOVA on the errors of poses P1 and P1 without wrist display showed a significant main effect of both the pose ($F(1, 11) = 12.346$, $p = 0.005$) and digit ($F(1.809, 19.9) = 7.12$, $p = 0.006$). There was no significant interaction between the digit and pose ($p = 0.417$). The errors for pose P1 without wrist display were on average approximately 1 cm larger than P1 for all fingers. We observed similar per-finger trends in error for Pose P1 without wrist display as the other poses. The 2×5 repeated measures ANOVA on area of the confidence ellipse showed an effect of the pose ($F(1, 11) = 13.65$, $p = 0.004$), but no significant effect of the finger ($p = 0.176$). There was no significant interaction between the finger and pose ($p = 0.059$).

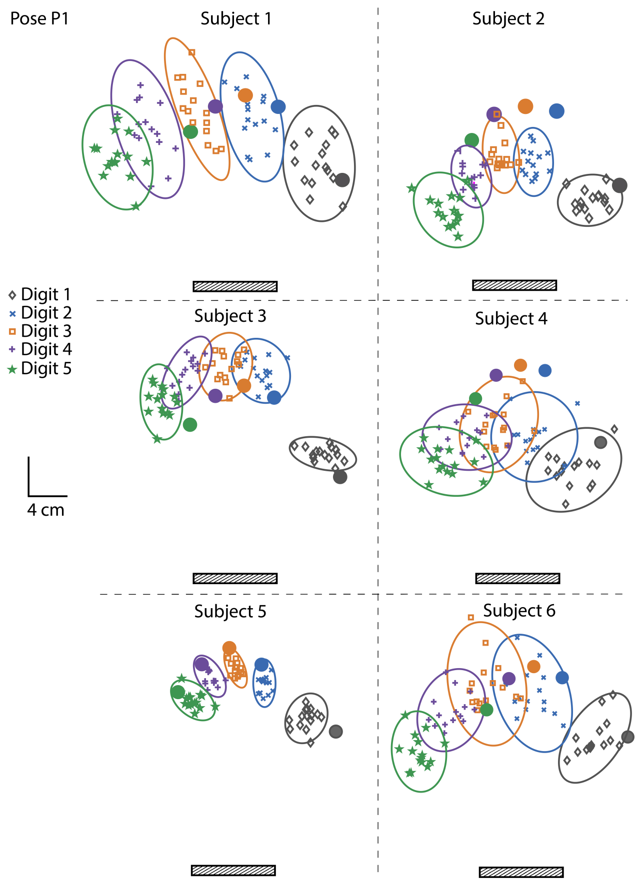

Fig. 4. Results for hand pose P1 for six subjects in Experiment 1. Subjects 1 and 6 show a consistent leftward bias in reported locations. Subjects 2 and 4 reported the fingers to be more proximal to the wrist than the veridical positions, while subject 3 reported the finger to be more distal. Each subject has a distinct error pattern, which illustrates the idiosyncratic nature of proprioceptive localization.

3 Experiment 2 : Visuo-Proprioceptive Integration in Localization of Fingers

The results of Experiment 1, if taken at face value, suggest that proprioception may provide location information that is too coarse, by itself, to accurately guide performance or learning in normal fine motor tasks, which commonly involve movements coordinated closely between multiple fingers. Thus, we sought to clarify how visual cues are integrated with proprioception in the estimation of finger locations. We hypothesized, and confirmed via pilot testing, that position estimates can be greatly improved if limited visual information about finger position is available, in contrast to the no-vision condition of Experiment 1. Thus, in order to study the integration of indirect visual cues and proprioceptive information in the localization of the fingers, we adapted the method of experiment 1 for a new study in which subjects reported the perceived positions of their fingertips with and without visual indicators as to locations of the other fingers. We also asked subjects to report the estimated position of a fingertip when visual indicators of adjacent fingertip locations were shown and no relevant proprioceptive information was available to the subject (because their hand was placed elsewhere), in order to assess the role of contextual visual information alone in estimating finger locations. In this experiment, we restricted our attention to digits 1 and 2 (thumb and index finger), since they are very commonly used to perform fine manipulation tasks in daily activities.

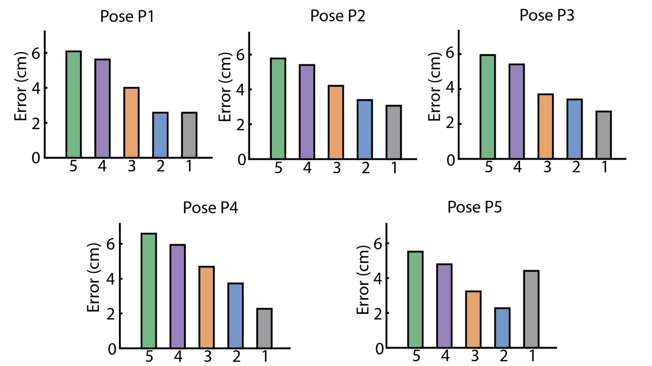

Fig. 5. Per-finger errors for all distinct hand poses (P1 to P5) for one subject in Experiment 1. The x axis indicates the digits of the hand. For most hand poses (P1 to P4), the localization of the thumb and index finger was the most accurate (mean 2.96 cm and 3 cm respectively), and the errors get progressively larger from digits 2 - 5, with the little finger having the largest errors (mean 5.96 cm). We observed large errors (4.5 cm) in the localization of the thumb in pose P5, when the thumb is placed in an extremely flexed position.

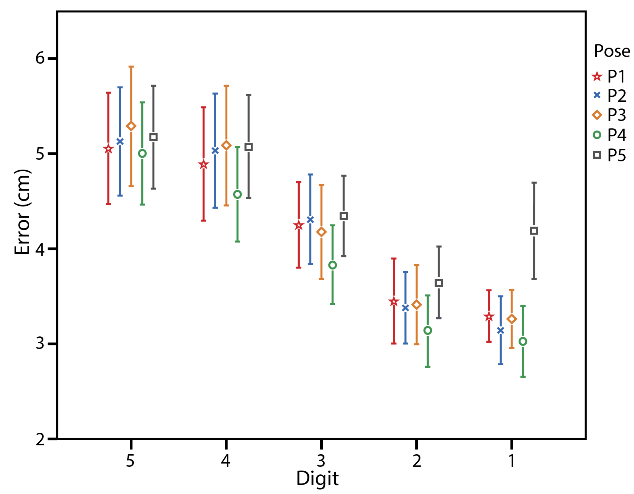

Fig. 6. Errors for each discrete hand pose (P1 to P5) averaged across all subjects in Experiment 1. The error bars show the Standard Error of the Mean (SEM) across subjects. Error patterns similar to those in Fig. 5 were observed, showing that they generalize across subjects. The localization errors of the thumb and index finger were similar, as were the errors of the ring and little fingers.

3.1 Methods

3.1.1 Subjects

Eight volunteers (6 male; 24 to 29 years of age) participated in the experiment. Four of them also participated in Experiment 1. All subjects were naive to the purpose of the experiment, had (corrected-to-) normal vision and gave their informed consent. One subject self-reported both hands to be dominant, with the others reporting their right hand to be dominant. The experiment was approved by the human subjects research review board of the University of California, Santa Barbara.

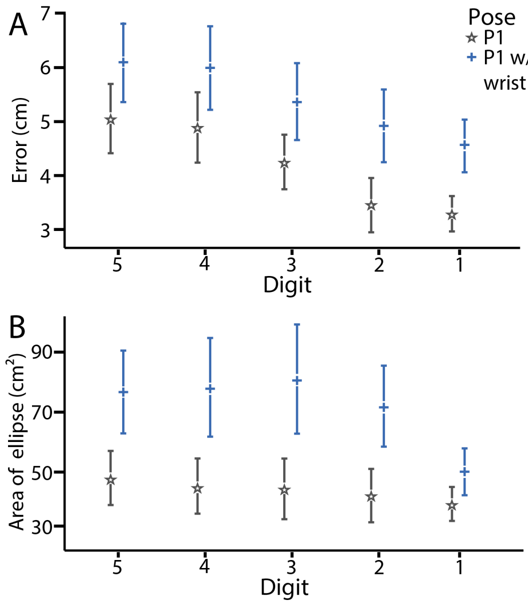

Fig. 7. A) Errors and B) area of the confidence ellipse for poses P1 and P1 without wrist display, averaged across all subjects in Experiment 1. The error bars show the standard error of mean (SEM) across subjects. The errors for pose P1 without wrist display were on average 1 cm larger than that of pose P1 for each finger. The areas of the ellipse for pose P1 without wrist display were on average 12 cm^2 larger than that of pose P1.

3.1.2 Apparatus

The experimental apparatus was identical to that used in Experiment 1, except that in Experiment 2, additional visual indicators, in the form of virtual markers (diameter: 8 mm), could be placed at the locations of fingertips.

3.1.3 Target hand Poses

A set of four unique hand poses (P1 to P4) was used (Fig. 8A) to discourage memorization of locations. The thumb and index finger were grouped as one unit, with other fingers grouped into another unit. The poses consist of combinations of flexing and extending each unit. Poses were specified as a set of fingertip positions, as in Experiment 1.

3.1.4 Procedure

During each trial of the experiment, the experimenter moved the subject's fingers to the hand pose with specified planar fingertip positions that were automatically projected onto the table, after which the subject held his or her hand at this location. The experimenter ensured that none of the subject's fingers were touching the others to limit the cutaneous cues available to the subject. The fingertip positions were recorded at this stage. A cursor, in the form of a small sphere that was controlled by the mouse appeared at a randomized location. Subjects were prompted to use the mouse and cursor to select the perceived location of the fingertip. Once the position was reported, a new hand pose was selected, and the next trial started.

The experiment consisted of three conditions (P, V, P+V). In the P condition, the perceived location of the fingertip was reported solely through proprioceptive information, and no visual cues are provided. In the V condition, the subject's hand was placed about two feet away from the table by fully extending the elbow joint, thus minimizing the role of proprioception in the task. Visual cues corresponding to the locations of fingertips for a hand holding a pose on the table were shown, with one fingertip location withheld (Fig. 8B). Subjects were asked to report their best estimate of the location of the missing fingertip based on the information provided to them. In the P+V condition, visual cues of the location of all other fingertips were provided, and perceived positions were reported using a combination of visual and proprioceptive information. In each block of trials, the subject reported the perceived location of one of either the thumb or index finger per condition, for a total of six blocks (3 conditions × 2 digits). Each of the four hand poses was repeated 15 times in each of the six blocks of trials, for a total of 360 trials per subject. Subjects received short breaks between each block of trials. Within each block, the poses are presented in block-randomized order, with each hand pose presented once within a random ordering, before moving to the next set of four hand poses. The experiment lasted 90 minutes on average for each subject.

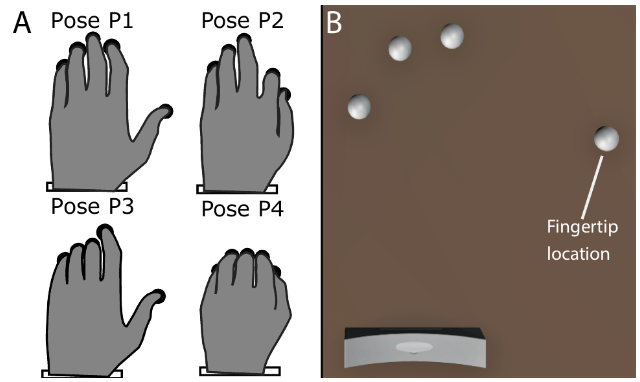

Fig. 8. A) Target Hand Poses used in Experiment 2. P1: Natural resting pose, P2: Thumb and Index finger flexed, P3: Middle, Ring and Little fingers flexed, P4: All digits flexed. The black circles are the target positions for the fingertips. Note that none of the fingers were touching each other. B) Top view within the virtual environment during one block of the V and P+V conditions, corresponding to Pose P1. The locations of the tips of digits 1, 3, 4, and 5 are shown via the displayed markers. Participants selected a location representing the missing digit. The wrist rest is shown at lower left.

3.1.5 Analysis

As in Experiment 1, we computed the magnitude of the mean error vector and a 95% confidence ellipse from each distribution of reported positions for the P and P+V conditions. The area A of the confidence ellipse was used to measure the random errors in localization. As multiple poses were utilized primarily to introduce variations in the task, and the results for Experiment 1 did not show a significant effect for pose, the pose was not used a factor for the analysis. The magnitude of mean error vector was averaged over all the poses ($E_{i,f}$) and compared for the P and P+V conditions, for both the thumb and index finger, by performing a 2 × 2 repeated measures ANOVA tests (Condition × Digit). Greenhouse-Geisser corrections were employed when sphericity was violated, and Bonferroni corrections were applied for the tests.

The V condition was used to study whether the distributions of finger positions with negligible proprioceptive

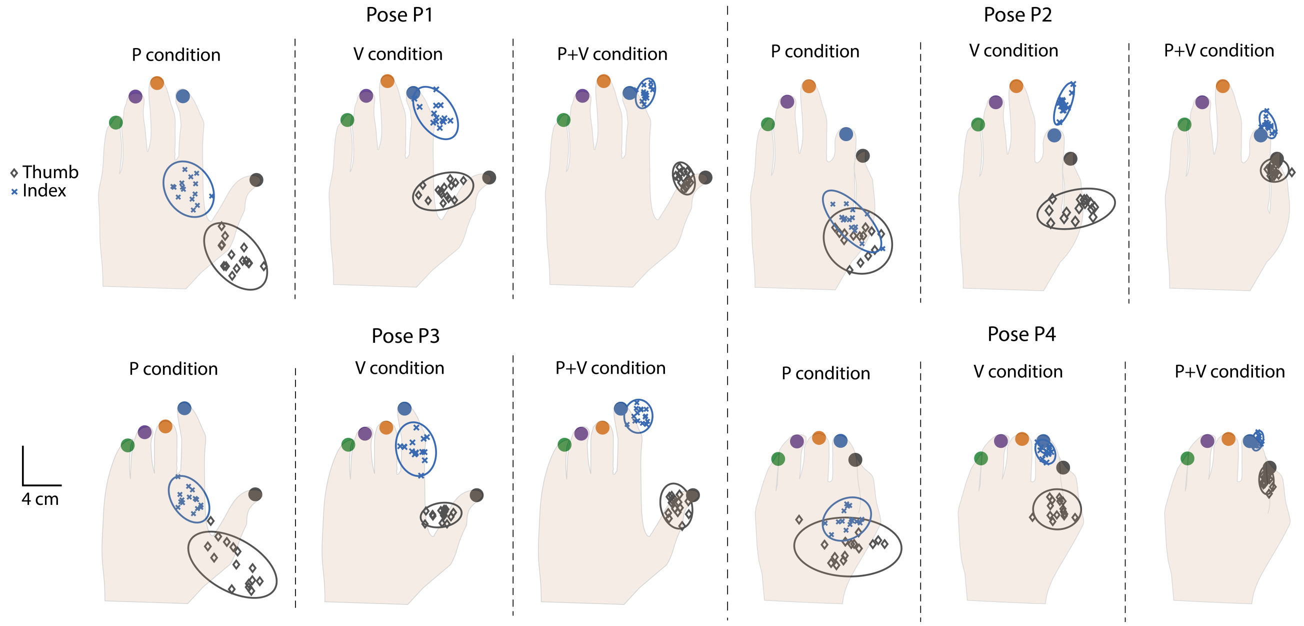

Fig. 9. Results for all poses and conditions for one subject in Experiment 2. The reported locations for the thumb and index finger for each pose and condition over all trials are overlaid to the same figure and are represented with specified markers. The ellipses are the 95% confidence ellipses. The error averaged over the two digits for the P condition was 7.38 cm, and the average area of the ellipse was 21 cm^2, For the P+V condition, average error was 1.31 cm, and average area of the ellipse was 3.9 cm^2. The subject was able to localize their fingertips more accurately when visual information of all the other fingertips locations were provided (P+V condition).

information and only visual cues (V condition) are combined with the distribution of finger positions obtained through proprioceptive cues (P condition) through linear multi-sensory integration models to obtain the combined percept (P+V condition). For this condition, as the ground truth position of the finger was not well defined, the error magnitude was not calculated. The area of the ellipse was computed in a similar fashion as the other conditions. The area of the confidence ellipse, when averaged over all the poses, was compared for all 3 conditions by performing a 3 $\times$ 2 repeated measures ANOVA tests (Condition $\times$ Digit).

3.2 Results

The reported positions and the confidence ellipses for all the conditions and target positions for one subject are shown in Fig. 9. The results for errors and confidence ellipse areas averaged across all subjects are shown in Fig. 10. Errors were significantly larger in the proprioception (P) condition when compared to the P+V condition (mean error 5.9 cm vs 1.54 cm, $p = 0.001$). The area of the ellipse was consistently larger for the P condition compared to the P+V condition (mean 49.8 cm^2 vs 7.8 cm^2, $p = 0.002$).

The results of the 2 $\times$ 2 repeated measures ANOVA test on the errors showed a significant main effect of the condition ($F(1,7) = 31.684$, $p = 0.001$), and no significant effect of the digit ($p = 0.453$). There was no significant interaction between the condition and digit ($p = 0.39$), which precludes within-factor analysis. Post-hoc pairwise comparisons for the condition showed that the errors for the P+V condition were significantly lower than those for the P condition ($p < 0.001$).

The results of the 3 $\times$ 2 repeated measures ANOVA test on the area of the confidence ellipse showed a significant main effect of the condition ($F(2,6) = 27.1$, $p < 0.001$), and no significant effect of the digit ($p = 0.097$). There was no significant interaction between the condition and digit ($p = 0.41$). Post-hoc pairwise comparisons for the condition shows that the areas for the P+V condition were significantly lower than those for the P condition ($p = 0.002$), but not significantly different from the V condition ($p > 0.5$). Further, the areas of the confidence ellipse for the V condition were significantly lower than those of the P condition ($p = 0.004$).

4 Discussion

The goal of Experiment 1 was to investigate multi-finger proprioceptive localization. We found the systematic errors (bias) and random errors in finger localizations to be large, implying that proprioceptive localization is neither very accurate nor precise compared, for example, with the typical length of the finger.

Our results suggest that the random errors of proprioceptive localization are similar for each finger. The systematic errors were smallest in magnitude for digit 1 and 2 (the thumb and little finger) and became progressively larger for subsequent digits, including digit 5 (little finger). The thumb and index finger are highly individuated and frequently used in precision grasping and manipulation. Consequently, it would appear that these estimates have developed to be the most accurate. The origin of large biases in proprioceptive estimates of finger locations is unclear. Plausibly, these positions could be calibrated through inputs from the visual system [26], [27], but it appears that large biases are allowed to persist.

While the dependence on pose was not significant, the mean errors and confidence ellipse areas were lowest for

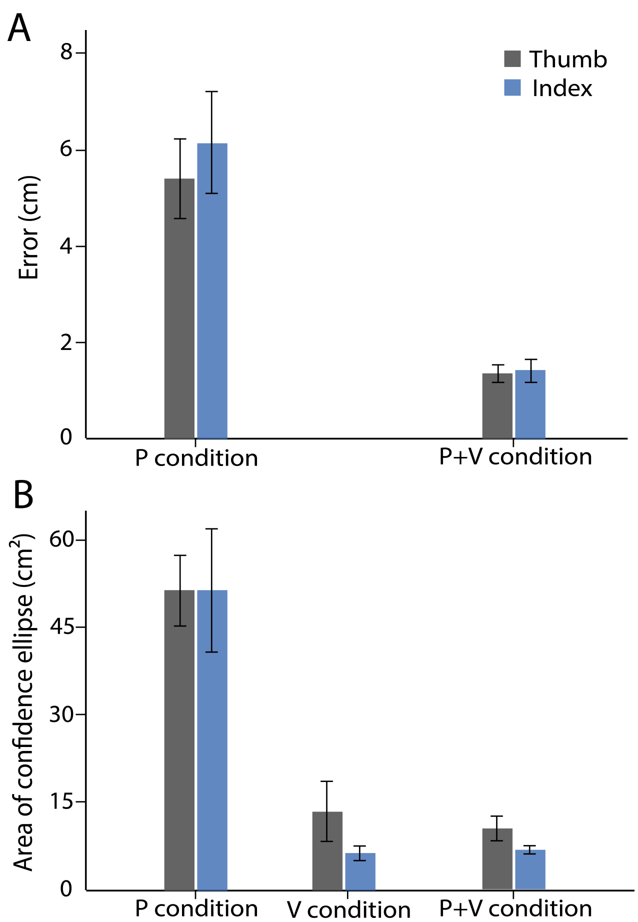

Fig. 10. A) Errors for the P and P+V conditions, for thumb and index finger, for all subjects in Experiment 2. B) Area of the confidence ellipse A for the P, V and P+V conditions, for thumb and index finger, for all subjects in Experiment 2. Error bars show the standard error of mean (SEM) across subjects. The localization accuracy in the P+V condition was significantly better than that obtained through either vision or proprioception alone. The random errors of localization in the P+V condition was significantly lower the P condition, but not the V condition.

pose P4, in which all fingers were flexed and the fingertips were closest to the wrist. The errors for the thumb were largest when it is at its most extreme position in pose P5. This suggests that, similar to proprioceptive localization of the whole limb [7], [8], proprioceptive localization of the fingers is more accurate for fingers that are closer to the body. An examination of the errors for pose P6 also shows that our effort to prevent accumulation of errors in the reporting for subsequent digits by randomizing the cursor location was successful, as the errors for digits 2 - 5 in this pose were not significantly influenced by the large errors of the thumb. This suggests that the reporting of finger locations was not dependent on previously reported positions.

The observed patterns of the systematic errors appeared to be idiosyncratic, and to vary across subjects, as illustrated in Fig. 4. The reported positions for various subjects differed both in error magnitude, and in the direction of the error patterns. We did not observe any systemic drift in proprioceptive estimates of finger locations for any pose over the course of either experiment (which lasted for a maximum of 100 minutes). In informal testing, we have observed that the error patterns remain consistent over the course of several weeks. This suggests that while the trial-to-trial variability in estimates is large, the proprioceptive map of the entire hand may remain stable, although further research is needed. These findings are analogous to those of prior studies that have shown that proprioceptive localization of the whole arm is idiosyncratic and stable [8], [14]. Informal testing also revealed similar patterns of errors for other reporting methodologies and hand positions, including methods which did not use a virtual environment.

The errors for all of the fingers were similar in magnitude to those that were reported for proprioceptive localization of the whole arm (3 to 6 cm) [7], [9], [14], even when the position of the wrist was displayed and was felt at the same location; this was true for all poses except P1 without wrist display. We had hypothesized that when the location of the wrist was displayed, the brain would be able to incorporate this knowledge to greatly aid the location estimates of the fingertips, making them more accurate, as the location of the arm would not need to be independently estimated. Based on the accuracy of fine motor behavior and that of various perception tasks (such as precision grip aperture size estimation), we had expected these errors to be on the millimeter scale. However, we observed that localization errors remained large (2.8 to 4.8 cm) when the wrist location was shown, and that the error patterns were similar to those we observed without this information. The magnitudes of the errors are especially striking when we consider that the average length of the hand is only 18 cm, and the average width only 10 cm. This could indicate that the brain does not use prior knowledge of parts of the body to directly refine proprioceptive estimates, suggesting that there exists in the CNS independent body schemas obtained through vision and proprioception, information from which would be combined to give position estimates, akin to the modular theory detailed by Tagliabue et al. [28]. A statistical comparison of the results for poses P1 and P1 without wrist display, which differ only in visual information about the wrist, does indicate that errors increased significantly in magnitude ($p = 0.005$) when the wrist location was not shown, but those errors were only 1 cm larger on average. This difference is much smaller than the errors in localizing the wrist. We hypothesize, based on post-experiment written reports of the subjects, that one of the reasons why both the errors and the confidence ellipse areas of pose P1 were smaller than those in P1 without wrist display was because subjects could notice that a proposed finger location estimate was implausibly close to the displayed location of the wrist for pose P1, which could affect their reported positions. In short, the effect of visual information about wrist location was significant, but small, contrasting with the larger effects observed in Experiment 2, as discussed below.

In Experiment 1, we also observed that the mean position estimates were more proximal to the wrist than the veridical fingertip locations, with digit-wrist distances being underestimated by 10% on average. The distances between the tips of digits 1 and 2 (thumb and index finger) are underestimated by 12%, while the 2-3, 3-4, and 4-5 inter-digit distances are overestimated by 28%, 46% and 13% respectively. This may suggest that the implicit map of the hand generated from proprioception is distorted from the true shape of the hand. The results are similar, in this respect, to those reported by Longo and Haggard [29] who found that the implicit hand representation for a single hand pose was widened (mean 67% overestimation of distance between knuckles) and shortened (mean 28% underestimation of finger length). From the results of pose P5, we observe that the inter-digit distance may generally depend on the pose of the hand. This distorted hand shape is also apparent when examining the results of many individual trials, possibly suggesting that an internal representation of the hand was employed in the perceptual task. This raises the question of whether proprioceptive estimates for each finger are independent. We explored this question by computing the standard deviation of the inter-digit distances across trials, the average of which was 1.2 cm. This result is larger than that expected if the reported positions for each finger were fully correlated, but is only marginally larger than the errors observed in our control experiment. This question would therefore necessitate a more focused study than ours to conclusively answer.

In Experiment 2, we observed that the localization in the "vision only" condition involves very small random errors, which seems to indicate that our subjects had a very precise visual estimate of where the finger could be positioned based on visual cues. The results for the "proprioception + vision" condition show that visual cues indicating the positions of adjacent fingers can greatly affect localization of unseen digits. Both random and systematic errors of localization improved significantly when this indirect visual information was available. This suggests that even partial visual information can greatly aid localization of the fingers. Such partial visual information could be available in conditions in which some digits are occluded from view, such as during object grasping and manipulation, or when visual attention is constrained. Thus, despite the limitations of proprioceptive sensing that this study brings to light, it can be improved by indirect visual cues; in our experiment, the mean errors and confidence ellipse areas declined to 1.54 cm and 7.8 cm^2 respectively with this information. This suggests that proprioceptive information about finger position, however coarse, may aid manual activities, although further research is needed in order to assess this in more complex and dynamic tasks, where proprioception may become more accurate, due to active movement.

As illustrated in Fig. 9, the position estimates in the condition in which both proprioception and visual cues were available did not generally lie between the estimates obtained separately in each unimodal condition. For this reason (as further reflected in our analyses), the results observed would not be consistent with models of multisensory integration that involve a weighted combination of unimodal estimates, such as simple linear weighted cue combination models, or maximum likelihood models, although other models of cue integration may be consistent with these findings. However, we note that in the "vision only" condition here, in addition to vision, participants also had access to (conflicting) information from proprioception from their hand, which was resting elsewhere. Thus, even though participants were instructed to ignore this proprioceptive sensory input as "irrelevant", it is unclear how it may have affected their responses. Further research is needed in order to clarify the integration of direct or indirect visual cues and proprioceptive information in the localization of the fingers.

5 Conclusion

In this study we investigated the proprioceptive localization of multiple fingers of the hand using somatosensory information alone, and in combination with visual cues as to the locations of the other digits. Proprioceptive position estimates exhibited large random and systematic errors. The latter were on the order of several centimeters. This was true even when the location of the wrist is displayed. Participants did not fare much better at locating their fingers relative to their wrist than they have been reported to do at locating the wrist itself. The observed errors were finger-dependent, with the localization of the thumb and index finger being most accurate. The hand shape implied in the data would be compatible with an internal representation that is biased and distorted, consistent with prior research, but which may be well maintained over time. When visual cues as to the locations of adjacent fingers was available, the errors decreased markedly. This suggests that the perceptual system is able to integrate bimodal information to improve position estimates even when body parts are occluded.

The results of this research suggest that the perceptual system can integrate discordant representations of finger position. This may be important for the sensorimotor control of grasping. It also suggests that in applications such as human-computer interaction or virtual reality, users may be able to accommodate large visuo-haptic discrepancies in finger position, which may facilitate new interaction techniques, rendering methods for representing the hands, or other interesting effects.

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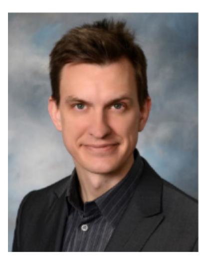

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