

Vision in the palm of your hand

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ABSTRACT

Here we show that pointing movements made to visual targets projected onto the palm of the hand are more precise and accurate than those made to targets projected onto back of the hand. This advantage may be related to the fact that the number of cortical bimodal neurons coding both visual and tactile stimuli increases with tactile receptor density, which is known to be higher in glabrous than in hairy skin.

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The hand and face are among the most densely innervated regions of the body with respect to touch. There are a greater number of tactile receptors embedded in the skin of the hand and face than in other regions of the body (Edin, Essick, Trulsson, & Olsson, 1995) and there is a greater proportion of somatosensory cortex devoted to these areas relative to other body parts (Penfield & Boldrey, 1937). As a result, the skin of the hand and face has superior tactile perceptual resolution as evaluated by two-point discrimination tests (Weinstein, 1968).

Neurophysiological studies in the macaque monkey have revealed neurons in different brain regions that respond both to visual and tactile stimulation with overlapping receptive fields (RFs). These bimodal neurons have been found in the dorsal half of the ventral premotor cortex [PMv; a.k.a. the polysensory zone (PZ); Graziano & Gandhi, 2000], the ventral intraparietal sulcus (VIP), and the putamen (Graziano, Yap, & Gross, 1994). The skin and percutaneous space near the hands and face are represented more densely by these bimodal neurons than are the skin and surrounding space of other parts of the body. In short, there appears to be a correspondence between tactile receptor density and bimodal-cell density. Body parts with higher tactile receptor density have greater visual-

tactile bimodal representation than body parts with lower tactile density and perceptual resolution.

An interesting feature of visual-tactile neurons is that they can be recruited by a visual stimulus presented alone (i.e. without any accompanying tactile stimulation) on or near a body part, primarily the hand or face. Thus, the question arises as to whether or not the 'quality' of the representation of a purely visual stimulus presented on the skin is correlated with the tactile resolution of that skin. In other words, high bimodal-cell density associated with skin regions with high tactile receptor density could mean that visual stimuli that appear on or near these regions would be represented more robustly than visual stimuli presented on or near skin regions with low tactile receptor density.

To test this possibility, we asked healthy undergraduates to perform visually guided pointing movements with their right hand to targets presented on their palm or on the back of their left hand. We chose this task to measure target quality because we know that measures of pointing accuracy and precision are sensitive to the location of targets defined using tactile and noxious stimuli (Koltzenburg, Handwerker, & Torebjork, 1993; Moore & Schady, 1995). Moreover, it seems likely that bimodal neurons evolved for the control of visually guided movements in concert with tactile information (e.g. Graziano & Cooke, 2006). Palmar glabrous skin has an estimated mechanoreceptor density of approximately 70 units/cm², providing this surface with high tactile acuity (Johansson & Vallbo, 1979). In contrast, the less sensitive hairy skin on the back of the hand has an estimated tactile receptor density of less than 5 units/cm² (Macefield, 1998). If the relationship between

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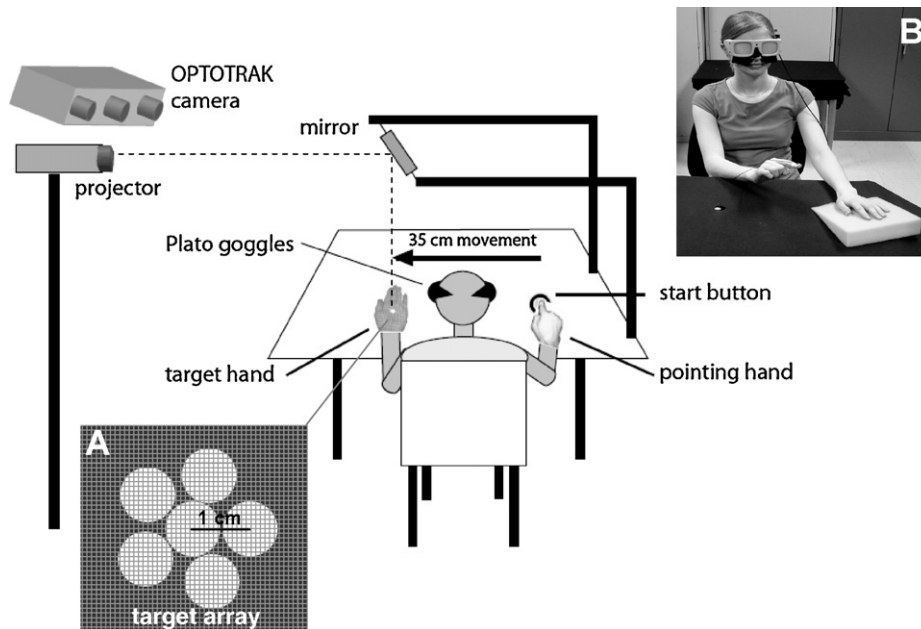


Fig. 1. Experimental Setup. The projector and mirror were used to project target circles onto the glabrous or hairy skin of the participant's left hand or a fake hand. The Plato LCD shuttered goggles were used to control the participant's view of the target and movements. Movements were tracked with the OPTOTRAK™ motion analysis system. Inset A shows the array of target locations that were presented singly in random order on each trial. Inset B shows a participant making a leftward movement to a target location on her own hairy skin without visual feedback (the PLATO goggles are occluding vision). This picture differs from the experimental situation in that during the experiment, the only lighting was from the projector.

tactile innervation and bimodal-cell representation of skin region extends to the different surfaces of the hand, the difference in tactile receptor density between the glabrous and hairy skin could be linked to a difference in bimodal-cell representation, and in turn to differential processing of visual stimuli presented on the glabrous and hairy skin. Thus, we predicted that visually guided pointing movements directed at visual stimuli presented on the palm would be more accurate and precise than similar movements

made to visual stimuli presented on the back of the hand, even in the absence of tactile feedback. To establish a baseline and to control for the possibility that participants could use visual landmarks to locate targets on the glabrous- or hairy-skin surfaces, we had participants point to targets on a convincingly realistic fake hand as well as to targets on their own hand (see Fig. 2). We predicted better overall pointing performance to targets presented on the real hand.

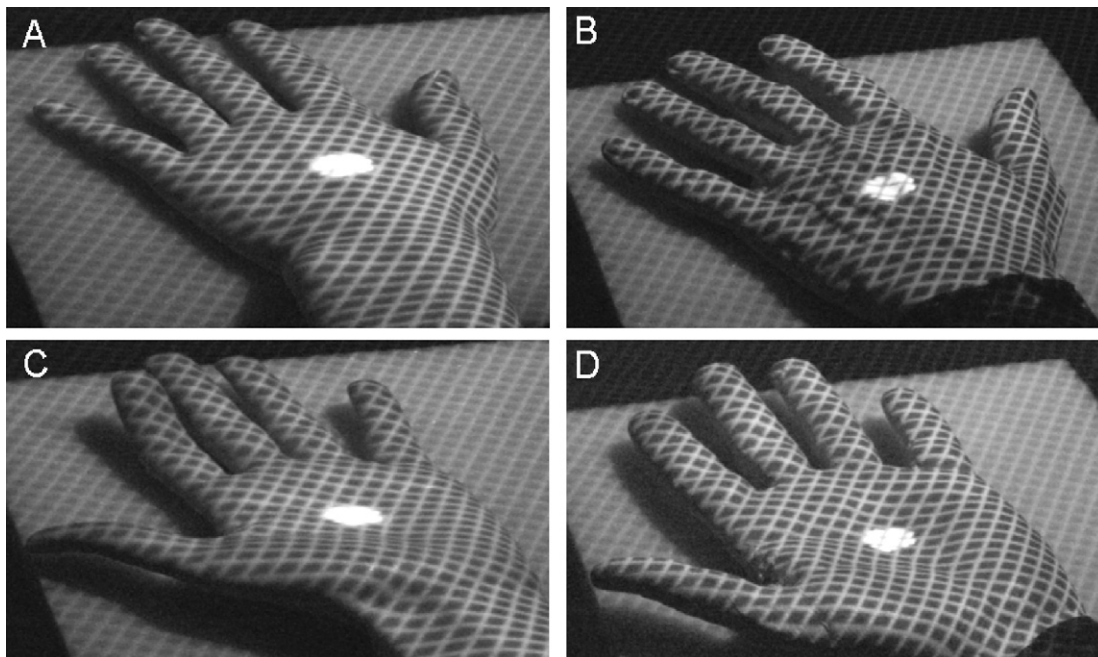


Fig. 2. Participants pointed to visual targets projected onto the hairy or glabrous skin of their own left hand (inset, Panels A and C, respectively) or onto the hairy and glabrous surfaces of a realistic replica of a left hand (inset, Panels B and D, respectively).

1. Methods

1.1. Participants

Sixteen healthy undergraduates (8 female) participated in this study in exchange for research-participation credit. All participants were right-handed. All participants provided informed consent before participating in the study.

1.2. Apparatus

Visual targets were projected by an LCD projector (InFocus) onto an angled mirror that was suspended over the target hand (see Fig. 1). The mirror reflected these visual targets onto either the participant's own real left hand or a realistic left-hand replica (Anytime Costumes) that was secured comfortably to the table below with a Velcro™ strap. The fake hand was constructed of dense, heavy foam. On the glabrous-skin side, it was detailed with skin-like surface features that included the high-spatial-frequency finger- and palm-print texture and all of the major low-frequency crease lines. Although the hairy-skin surface did not have hair, it did have knuckle indentations and raised areas depicting the finger-extensor tendons and surface veins (see Fig. 2). The room was dark except for the light coming from the projector itself. A custom-made start button, fastened to the table, was used to record the initiation of the pointing response and to trigger the closure of liquid-crystal display goggles (PLATO, Translucent Technologies) that were worn by the participants. The PLATO goggles were used to control stimulus-exposure time. An infrared-emitting diode (IRED), attached to the tip of the participant's right index finger, was used to track the trajectory of the pointing movements. The IRED was tracked with an OPTOTRAK™ 3D motion analysis system (Northern Digital Inc., Waterloo, Ontario, Canada). The OPTOTRAK™ recorded the three-dimensional position of the IRED at a frequency of 200 Hz. The positions were saved and later analyzed off-line.

1.3. Stimuli

The targets appeared as bright, white circles, 1, 2, and 3 cm in diameter. A visual texture was also projected onto the target surface in an additional effort to prevent participants from using glabrous- and hairy-skin surface features as cues for coding target location on the skin surface. Each target was projected to one of six different randomly chosen locations on the glabrous- or hairy-skin surface of the palm of the hand. Six target locations were used to minimize the participants' tactile memory for target location over the course of the experiment. A center target position was encircled by five surrounding positions, which were each 1 cm away from the center position (see Fig. 1). The center of the palm and back of the hand were measured and aligned with the central target at the beginning of each block. Although the targets were projected onto the hand, the location of the targets in space was fixed and did not vary with the projection surface. The distance between the start button and the center target position was 35 cm. The center target position and the start button were both 20 cm away from the participant in depth (Fig. 1). It should be emphasized once more that the stimuli were entirely visual and there was no tactile information about target location.

1.4. Experimental design and procedure

The experiment followed a 2 hand-type (real, fake) by 2 skin-side (glabrous, hairy) by 3 target-size (1, 2, 3 cm diameter) × 6 target-location within-subjects design. Specifically, participants pointed to visual targets projected onto the glabrous (palm) or hairy (back) side of their actual left hand or onto the palm or back of the fake left hand. The four hand-skin conditions, real-glabrous, real-hairy, fake-glabrous, and fake-hairy, were presented in eight blocks of 36 trials. Block order was counterbalanced across participants. Within each block, target size and location were presented pseudo randomly such that each combination of target size and location was repeated twice. During the real-hand conditions, the fake hand was placed out of view and during the fake-hand conditions, participants' were instructed to place their own left hand below the table across their lap.

At the beginning of each trial, participants' vision was occluded. The target was projected onto the hand, and after a variable foreperiod (500–1250 ms), the PLATO goggles were opened and the participant heard an audible tone. Participants were instructed to initiate a quick and accurate pointing response to the center of the target, moving from right to left, upon hearing the tone. Response initiation was synchronized with the closure of liquid-crystal display goggles worn by the participant, occluding participants' vision and removing any opportunity to use vision to adjust the hand's trajectory en route. Although the instructions stressed movement speed and accuracy, not reaction time, participants were prevented from viewing the target for longer than 1000 ms. Participants were also instructed to make smooth pointing movements and to avoid making secondary, corrective movements. In any case, as described below, if corrective movements did occur, they were not included in the definition of the movement. Although participants did touch what they thought was the target location at the end of each pointing movement, they were never given the opportunity to compare their pointing performance to the actual target location. That is, they received no post-performance feedback about the accuracy of the movement they had just executed.

Although the physical location of the targets was fixed in space, it was possible that the projected location of the target may have differed between participants due to factors like the thickness of the hand. To address this possibility, we measured the location of each target on each participant's hand at the end of the experiment. Participants were given as much time as they needed to point to the center of the 1-cm target as accurately as possible. These pointing trials were performed with full vision of the target. These measurements were used as the standard for calculating pointing error within each individual participant.

1.5. Data analysis and dependent measures

The OPTOTRAK™ system recorded the position of the IRED in the x, y, and z dimensions over time. Analysis programs written with Matlab (The Mathworks, Inc.) were used to define the beginning and end of each pointing movement. The onset and the end of the movement were defined as the time when the resultant velocity of the index finger first exceeded or and then first fell below (respectively) 20 mm/s for five consecutive samples. Secondary corrective movements were excluded from the analysis. Measurements of movement time (MT), signed endpoint error in both the horizontal and depth dimensions, and endpoint error variability (standard deviation) of the right index finger were calculated. Each of these measures were submitted to repeated-measures analysis of variance. Interactions were decomposed by conducting simple main effects analyses. Main effects for factors involving more than two levels (target and location) were further investigated with Tukey's HSD post-hoc tests.

2. Results

Fig. 3 shows the final position of the pointing movements performed by all 16 participants in each of our four target-surface conditions: the hairy and glabrous skin of their own real hand (panels A and C) and the hairy and glabrous surfaces of the fake hand (panels B and D). We compared the resolution of the target repre-

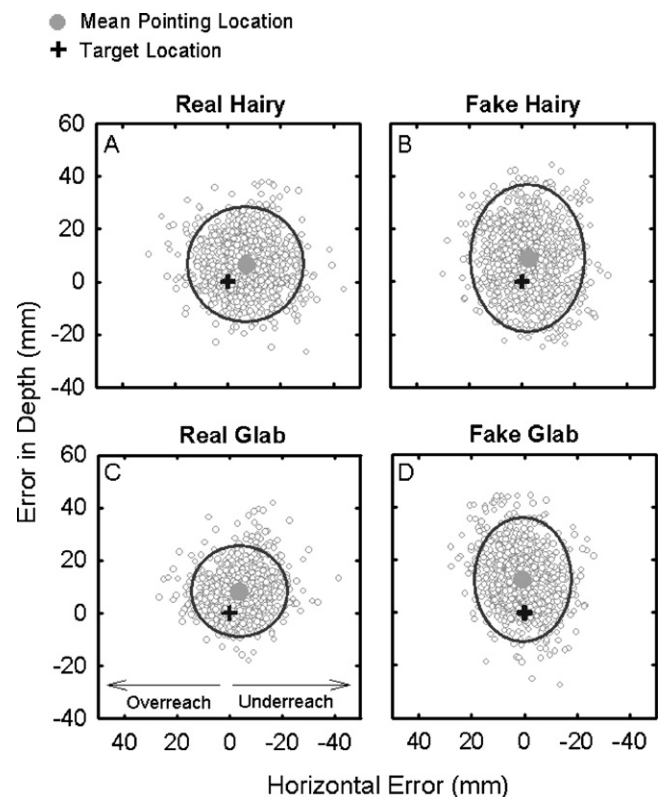


Fig. 3. Here we show the end position with respect to the target location (i.e. the pointing error) for every pointing movement for all participants (○) in each of the four target-presentation conditions—the hairy or glabrous (palm) skin of their own left hand (Panels A and C, respectively) or the hairy and palm “skin” surfaces of the fake left hand (inset, Panels B and D, respectively). The black cross (+) represents the target location, and the black filled circle (●) shows the average signed pointing error in each condition. The grey ellipses represent error variability, the 95% confidence interval of the error in the horizontal and depth dimensions.

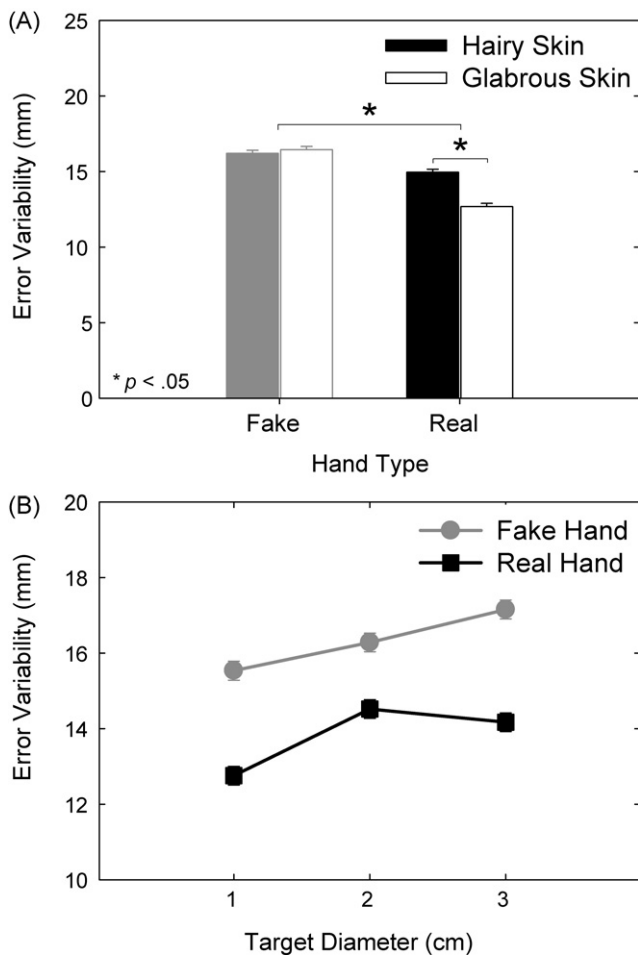


Fig. 4. (Panel A) Error variability as a function of hand type and skin side. Error variability was significantly reduced for pointing to targets on the glabrous skin over the hairy skin only when those targets were projected onto the real hand. (Panel B) Error variability as a function of target size and hand type. Error variability was significantly less on the real hand than the fake hand, and a significant increase in variability with target size was marginally attenuated when targets were presented on the real hand.

sensation in these four conditions by analyzing pointing variability, as measured by the mean absolute distance between the final pointing position and the target (i.e. the mean distance between the small grey circles and the center of the black circle for each of conditions in Fig. 3). This analysis revealed an interaction between hand type and skin side, $F(1, 15) = 9.56$, $p = .007$. As illustrated in Fig. 4A, pointing movements to the real hand were more precise to targets projected on the glabrous skin (mean \pm S.E.M.: $12.86 \pm .21$ mm) than on the hairy skin ($14.95 \pm .20$ mm), $F(1, 15) = 5.65$, $p = .031$, but when pointing movements were made to the fake hand, the precision of pointing to the glabrous ($16.45 \pm .21$) and hairy skin ($16.20 \pm .20$ mm) did not differ significantly, $F(1, 15) = .40$, $p = .537$.

Predictably, pointing variability increased with target size, $F(2, 15) = 4.29$, $p = .023$, and this effect interacted marginally with hand type, $F(2, 15) = 3.12$, $p = .058$, such that variability increases with size were attenuated for targets presented on the real hand in comparison to the fake hand (see Fig. 4B). There were no interactions involving target size, skin type, or target location (all $ps < .25$). There also were effects of target location, $F(5, 15) = 4.36$, $p = .002$, such that movements to the target nearest the start location of the movement ($16.94 \pm .23$ mm) were more variable than movements to all other locations (mean at 5 other locations: $14.71 \pm .24$ mm). This effect

interacted with both hand and skin, $F(5, 15) = 2.54$, $p = .035$, such that the variable error at this location was significantly reduced ($13.18 \pm .47$ mm) in the real-hand, glabrous-skin condition only.

These patterns were also reflected in the directional error variability. Directional error variability is represented by the ellipses shown in Fig. 3, whose vertical and horizontal radii represent the 95% confidence interval of the signed error along the depth (away from the body) and horizontal (along the axis of movement) dimensions, respectively. There was an interaction of hand type and skin side for pointing variability in depth, $F(1, 15) = 6.66$, $p = .021$. Again, for movements to the real hand, pointing precision in depth was greater for movements made to targets on the glabrous ($6.19 \pm .23$ mm) rather than hairy skin ($7.32 \pm .24$ mm), $F(1, 15) = 8.57$, $p = .01$, but this skin effect was not present for the fake hand, $F(1, 15) = .00$, $p = .993$ (“glabrous side”: $8.32 \pm .24$ mm; “hairy side”: $8.32 \pm .23$ mm). Error variability along the horizontal axis (the axis of movement) was affected by skin side, $F(1, 15) = 37.66$, $p = .001$, such that horizontal movement precision was greater for movements made to the glabrous side ($7.26 \pm .25$ mm) than to the hairy side ($8.71 \pm .24$ mm) of either the real or fake hand.

Analysis of the mean signed error along the horizontal axis of movement (from right to left) revealed that although participants were more likely to undershoot the target when pointing to their own left hand ($5.44 \pm .18$ mm) than to the fake left hand ($.80 \pm .18$ mm), $F(1, 15) = 25.40$, $p < .001$, this error was significantly smaller on the glabrous skin ($3.88 \pm .25$ mm) than on the hairy skin ($7.04 \pm .25$ mm), $F(1, 15) = 11.94$, $p = .004$. In the depth dimension, the mean signed error was smaller for targets on the real hand ($7.11 \pm .17$ mm) than on the fake hand ($10.45 \pm .17$ mm), $F(1, 15) = 6.06$, $p < .026$. These differences in accuracy cannot be attributed to a speed-accuracy trade-off, as movement times were marginally shorter for the real-hand targets than for fake-hand targets, $F(1, 15) = 3.04$, $p = .056$, and were marginally shorter for glabrous-skin targets than for hairy-skin targets, $F(1, 15) = 4.02$, $p = .063$.

Participants may have used tactile information from either the pointing finger (in all conditions) or from the target surface (in the real-hand conditions) to learn the tactile location of targets as trials were repeated, and it is possible that this learning was better in the real-hand, glabrous-skin condition than in other conditions. We used two methods to address the possibility that participants simply learned the six target locations by touch, and that this tactile learning was better for the glabrous than the hairy skin. First, when we analyzed only the first trial in each condition, we still found that movements directed at targets on the glabrous skin of the real hand ($12.01 \pm .49$ mm) were significantly more precise than those directed to targets on the hairy skin ($14.94 \pm .49$ mm), $F(1, 15) = 7.11$, $p = .018$, or on either side of the fake hand, $F(1, 15) = .87$, $p = .367$ (“glabrous side”: $15.19 \pm .50$; “hairy side”: $16.37 \pm .49$). Thus, precision was better in the real-hand, glabrous-skin condition even when there was no opportunity to use any kind of prior tactile experience about the location of the targets (see Trial 1 in Fig. 5). Second, we looked for evidence of tactile learning by assessing changes in error variability as trials were repeated within each condition (see Fig. 5). We found that there was no significant overall change in error variability as a function of trial repetition, $F(5, 79) = 2.25$, $p = .056$, and there was no systematic decrease in error variability between Trial 1 and Trial 2, $F(1, 15) = .033$, $p = .858$, or between Trial 1 and Trial 6, $F(1, 15) = .707$, $p = .412$. In addition, in both of these analyses, there were no significant interactions involving trial repetition. Thus, we found no evidence to suggest that participants used tactile learning as a strategy for reducing error variability in the real-hand conditions. Moreover, there is no evidence that participants used tactile learning as a strategy for reducing error variability in the real-hand-glabrous-skin condition over the real-hand-hairy-skin condition.

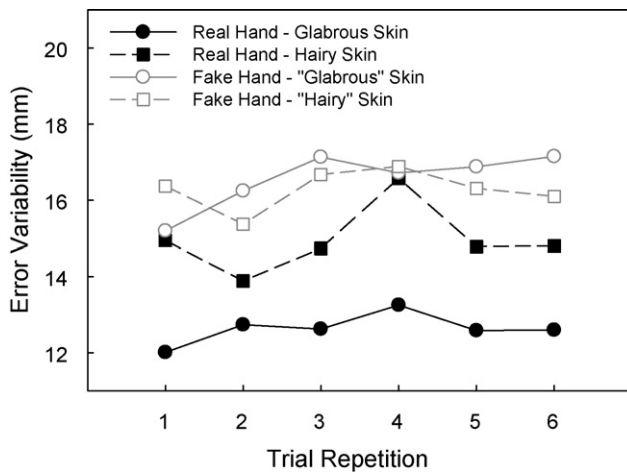


Fig. 5. Error variability as a function of trial repetition in each hand-skin condition. There was no systematic decrease in error variability between Trial 1 and Trial 2, or between Trial 1 and Trial 6. Therefore, we found no evidence suggesting that participants used tactile learning as a strategy for reducing error variability in the real-hand conditions over the fake-hand conditions, or in the real-hand-glabrous-skin condition over the real-hand-hairy skin condition.

3. Discussion

We believe that unimodal visual targets presented in the palm of the hand are represented more robustly because of links between tactile receptor and cortical density and visual-tactile bimodal-cell density in the cortex. In other words, skin regions that enjoy greater tactile receptor density and cortical representation are also more densely represented by bimodal neurons. Visual stimuli shown in the palm of the hand recruit bimodal neurons and these neurons contribute to a more robust visual representation of the target, allowing pointing movements to be performed more precisely to targets that appear in the palm of the hand. Kennett, Taylor-Clarke, and Haggard (2001) used a magnifying glass to exaggerate vision of the skin on the arm and showed that it improved tactile discrimination there. The complementary result we show here demonstrates that the more naturally occurring variations in skin tactile receptor and cortical density can have a tangible impact on how visual information on and perhaps near the skin is represented.

One alternative explanation for our results is that participants used skin-surface landmarks to locate the target with more precision and accuracy on the glabrous skin than the hairy skin of the real hand. There are several features in our experimental design that allow us to be confident that our effects cannot be explained by the possible visual surface-feature differences between the glabrous and hairy skin.

We used a convincing fake hand to control for the visual markings on the glabrous and hairy skin. This fake hand is so detailed that on the glabrous skin it has all of the major low-frequency crease lines on the palm and it had the high-frequency textural lines that are necessary to make a finger or palm print. Although the hairy surface does not have hair, it does have knuckle indentations and raised areas representing finger-extensor tendons and surface veins. Indeed, if anything, the landmarks provided on the hairy skin of both the real and fake hands were more prominent than those on the glabrous surfaces, yet there were no differences in precision or accuracy between the fake hairy skin and the fake glabrous skin, and there were significant advantages for the glabrous skin of the real hand, contrary to the predictions of a landmark-based localization hypothesis.

Finally, to reduce the possible impact of landmarks on performance, we masked all of these surface details by projecting a high

contrast grid pattern onto each target surface. We believe the grid was equally effective at obscuring skin landmarks on the real and fake hands. Moreover, because the grid and the target were projected onto the skin in a darkened room, the contrast between the target and the grid was identical on the palm and hairy surface of both the real and the fake hands. Taken together then, the differences in the visual features of the target surfaces do not appear to capture the pattern of data presented, i.e. the superior precision and accuracy of pointing to targets presented on the glabrous skin of the real hand.

The superior performance with targets presented on the real as compared to the fake hand may reflect not only a difference in visual processing but also the fact that proprioceptive information would have enabled participants to localize the position of their real hand but not the fake hand. Proprioceptive information would have been particularly useful for determining hand position in depth (van Beers, Sittig, & Van Der Gon, 1999). Proprioceptive and tactile contributions to hand localization cannot, however, account for the fact that participants were both more accurate and more precise in pointing to targets on the glabrous rather than the hairy skin of their real hand. Although muscle length- and force-receptors, and proximal-joint receptors and skin deformation, provide proprioceptive information about the relative position of distal limb segments, it is unlikely that they provide differential information about the location of particular areas of skin on those distal limb segments. Moreover, because presenting targets on the hairy skin of the real hand required that the glabrous skin be compressed as the hand was stabilized, and vice versa, tactile contributions to hand localization should have been more robust in conditions when targets were presented on the hairy skin rather than the glabrous skin.

It is possible but unlikely that participants used some sort of tactile imagery strategy. If this was true, intersubject variability would have been large due to individual differences in imagery ability and strategy. One would still need to map the visual stimulus onto the tactile map, without the benefit of any tactile stimulation. In short, this seems a far less parsimonious explanation, given the primacy of vision for target-directed movements and the complete absence of any tactile cues in this task.

The superior performance with visual stimuli presented on the real hand, particularly on the glabrous surface of the hand, may reflect the role of bimodal cells in the fine motor control related to object manipulation. In many tasks, the left hand is used to stabilize the object of interest while the right hand is used to act upon and manipulate that object and its parts (Sainburg, 2005). Bimodal cells may therefore have evolved in the context of manual interactions. In addition, the important role of the hands in feeding, particularly in primates, may also have been a significant factor in the emergence of visuotactile cells not only in association with the hands but also the mouth and face. In future studies, it would be of interest to explore differences in the engagement of these putative bimodal mechanisms between the left and right hands, reflecting the different roles the two hands play in the manipulation of objects.

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