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Research Report

Precise tactile localisation of hair stimulation in humans

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ABSTRACT

Hair is a salient feature of the bodies of humans and other mammals, which serves a variety of functions, including sensation. The sensory functions of hairs in humans, however, remain poorly understood. This study measured the ability to perceive the spatial location of stimulation of hairs without associated stimulation of the skin. We tested this ability body on the hand (Experiment 1) and the forearm (Experiment 2). Participants judged locations by clicking on a picture of their own hand/arm. We compared tactile localisation performance following hair stimulation to direct stimulation of the skin. Participants showed highly precise localisation of hair stimulation. The precision of localisation of hair stimulation is similar to that of stimulation of the skin. The results of this study show that human hairs provide rich spatial information which may complement tactile signals from the skin itself.

Hair is an important feature of mammalian bodies. Hair covers the majority of the body surface in most mammals and likely serves a wide range of functions, including regulating body temperature, camouflage, and protecting the body from mechanical insult and sun damage (Buffoli et al., 2014; Sandel, 2013). Hair also has sensory functions (Lechner & Lewin, 2013), and hairs and hair follicles are linked to a range of mechanoreceptors (Handler & Ginty, 2021). Indeed, fossil studies of brain evolution have linked the emergence of the cerebral cortex in early mammals to the emergence of fur, suggesting that sensory processing of hair deflection may have been central to brain evolution (Rowe et al., 2011).

In a classic study, Zotterman (1939) showed that gentle strokes of cat fur evoke several types of afferent signal travelling to the central nervous system at different speeds. A subsequent study of cats and rabbits by Brown and Iggo (1967) showed that myelinated Aβ fibres function as movement detectors, with the intensity of firing related to the velocity of movement across the limb. The hairy skin is also innervated by a class of unmyelinated C-tactile (CT) afferents both in animals (Iggo, 1960; Kumazawa & Perl, 1977) and humans (Vallbo et al., 1999). These CT afferents also respond maximally to moving stimuli, showing a preference for moderate velocities between 1 and 10 cm/sec which humans tend to find pleasant (Löken et al., 2009).

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More recent research has used genetic labelling to investigate the innervation of hair follicles in mice. Each of the three main types of hair (guard hairs, awl/auchene hairs, and zigzag hairs) is innervated by a unique combination of low-threshold mechanosensory receptors (LTMRs), including myelinated Aδ and Aβ LTMRs as well as unmyelinated C-LTMRs (Li et al., 2011; Li & Ginty, 2014). This suggests that each of these hair types acts as a specialised sensory receptor. Other research has found that high-threshold mechanosensory receptors (HTMRs) sensitive to pulling of hairs have highly-localized receptive fields that tile the skin surface, suggesting that they are involved in localisation of painful stimuli (Ghitani et al., 2017). Recent research in humans has shown that epithelial cells lining the inner surface of hair follicles act as transducers converting mechanical deflection of hairs into stimulation of sensory neurons (Agramunt et al., 2023). The density of hair follicles in humans varies dramatically across the body surface (Szabo, 1967), and correlates closely with the innervation density of fast-adapting fibres (Corniani & Saal, 2020). Single afferents in humans are linked to groups of 20–25 hairs on both the forearm (Vallbo et al., 1995) and hand (Corniani & Saal, 2020). A recent study showed that the density of hairs across different regions of the face corresponds to the locations where people tend to touch their face (Grunwald et al., 2025).

Microelectrode recordings in cats have shown that neurons are responsive to deflection of single hairs, both in the spinal cord (Yamamoto et al., 1956) and the somatosensory cortex (Adrian, 1941; Mountcastle, 1957; Mountcastle et al., 1957). Mountcastle (1957), for example, found separate populations of neurons in cat somatosensory cortex which responded to deflection of hairs and to pressure on the skin. Remarkably, the hair-sensitive neurons outnumbered the pressure-sensitive ones by a factor of four, though there were also a set of neurons with more complex response properties. Mountcastle showed, further, that both of these types of neurons, as well as others selective to joint movement or deep sensibility were organised into modality-specific cortical columns, each of which showed an overall somatotopic organization across the primary somatosensory cortex. Subsequent research has reported similar results in monkeys, with neurons responding to stimulation of hairs found in the thalamus (Kaas et al., 1984), primary somatosensory cortex (Tanji & Wise, 1981), and secondary somatosensory cortex (Robinson & Burton, 1980), as well as in the primary motor cortex (Strick & Preston, 1978).

Together, this research shows that mammalian hairs are equipped with a rich sensory apparatus which carries information to the brain that could be used for a variety of perceptual functions, including spatial localisation and discrimination. However, little if any research has investigated spatial perception from hair stimulation in humans. There are likely a couple of reasons for this. First, the complete absence of hairs on the glabrous skin which features most conspicuous tactile discriminative sensitivity – such as the fingertips and lips – demonstrates that hair is not necessary for discriminative touch. Moreover, that such regions have evolved in primates to be hairless suggests that hair may actually be maladaptive for spatially precise discriminative touch. Second, the tuning of CT afferents in hairy skin to velocities (Löken et al., 2009) and temperatures (Ackerley et al., 2014) of touch consistent with interpersonal stroking has led to stimulation of hairs being associated with affective, rather than discriminative, touch (McGlone et al., 2014).

The sensory functions of hairs are not limited to mammals, but appear to be strikingly widespread throughout the animal kingdom (for review, see Boublil et al., 2021). For example, in insects, specialised clusters of hairs known as hair plates play an important role in proprioception and sensory guidance of movements (Tuthill & Wilson, 2016). Sensory hairs are also used to monitor air flow to control flying in insects such as locusts (Weis-Fogh, 1949) and cockroaches (Fraser, 1977), as well as in bats (Sterbing-D'Angelo et al., 2011). Similarly, sensory hairs are used to detect water flow in crustaceans such as crayfish (Tautz et al., 1981), and in marine mammals like whales (Drake et al., 2015) and manatees (Reep et al., 2002). Thus, across the animal kingdom hairs serve a wide range of sensory roles, both to detect and localise stimuli, and to monitor and control ongoing motor behaviours.

One important example which clearly demonstrates that hairs can be used for precise spatial localization is whiskers. Whiskers are specialized hairs on the face of many mammals which provide rich sensory information about the world. Rats are able to use tactile signals from their whiskers for many tasks, including navigating through mazes (Vincent, 1912), discriminating textures (Carvell & Simons, 1990; Guić-Robles et al., 1989), recognizing objects (Brecht et al., 1997; Harvey et al., 2001), perceiving object orientation (Polley et al., 2005), maintaining body posture while swimming (Ahl, 1982), judging depth (Jenkinson & Glickstein, 2000), perceiving the width of apertures (Krupa et al., 2001; Shuler et al., 2002), and localizing objects in space (Diamond et al., 2008; Knutsen & Ahissar, 2009).

The use of whiskers for tactile localization in rats provides a clear demonstration that hairs can in principle support highly precise tactile localization. At the same time, whiskers are highly specialized hairs, which are clearly not representative of other hair, such as that on humans. One important point is that rats use active whisking movements to explore their environment (Sofroniew & Svoboda, 2015), which are critical for tactile localization with whiskers (Knutsen et al., 2006; Mehta et al., 2007). While rats may be able to tell where along the length of a whisker a touch was located with passive stimulation (Krupa et al., 2001; Pammer et al., 2013), localization in the horizontal and vertical axes appears to require active whisking movements (Knutsen et al., 2006).

Hairy skin in humans is innervated by a range of afferents, including myelinated Aδ and Aβ fibres and unmyelinated C-fibres. Mancini et al. (2011) showed that tactile localisation ability in humans is similar for stimulation of Aβ (innocuous touch), Aδ (pinprick heat), and C fibers (nonpainful heat). As described above, hairs are innervated by various combinations of each of these receptors. Thus, human hairs are innervated by multiple types of afferents which are known to support localisation ability. This provides good reason to predict that stimulation of hairs, without stimulation of the skin itself, can support tactile localisation, but this has not been empirically investigated.

The present study investigated the ability of humans to precisely localize stimulation of hairs. Neurocognitive models of somatoperception (Longo et al., 2010; Medina & Coslett, 2010) have emphasized that tactile localization is a distinct process from more basic features of touch such as detection, consistent with reports of selective impairment of tactile localization following brain damage (Halligan et al., 1995; Head & Holmes, 1911). We used an established paradigm for measuring tactile localization (Mancini et al., 2011) to assess localization ability when stimulation was limited to brushing of hairs on the hand dorsum (Experiment 1) and forearm (Experiment 2). Localization performance following hair stimulation was compared both to chance levels and to performance following direct stimulation of the skin.

1. Methods

1.1. *Participants*

Nineteen individuals (8 women, 11 men) between 21 and 39 years of age (*M*: 26.8, *SD*: 4.8) participated, after giving written informed consent. The same participants completed both experiments in a single experimental session. Handedness was measured using the Edinburgh Inventory (Oldfield, 1971). All participants except one were right-handed (*M*: 77.2, *SD*: 44.4). Data from one additional participant was excluded from analyses on account of the photograph of the actual stimulus locations being missing. Procedures were approved by School of Psychological Sciences Research Ethics Committee at Birkbeck.

The determination of sample size used the same logic as in the recent study of tactile localisation on fingernails (Longo, 2024). This experiment asks whether people can spatially localise stimulation of hairs at all. This question is similar to the study of Miller et al. (2018) who investigated the tactile localisation on held tools. Miller and colleagues quantified performance by regression judged location along the rod on actual location. At chance, regression slopes should equal 0; with optimal performance they should equal 1. Localisation ability can thus be tested by comparing mean regression slopes to 0 using one-sample *t*-tests.

While previous studies using this paradigm to localise touch on the hands did not analyse their data in this way, we analysed data from the study of Margolis and Longo (2015) to estimate an effect size for a power analysis, which was very large ($d = 3.751$). We aimed to be able to detect performance from hair stimulation one quarter the size of the skin, and so divided this effect size by four (i.e., $d = .938$). We used this effect size to conduct an a priori power analysis with G*Power 3.1 (Faul et al., 2007) for a two-tailed, one-sample *t*-test with alpha of .05 and power of .90. This analysis indicated that 15 participants were required. To be safe, we recruited 20 participants, with data from 19 ending up being useable.

1.2. *Procedures*

Experiment 1. The procedures were similar to previous studies using this paradigm (Kang & Longo, 2023; Longo, 2024; Longo et al., 2015; Mancini et al., 2011; Margolis & Longo, 2015; Medina et al., 2018). A 3 × 3 grid of points was drawn onto the dorsum of the participant's left hand using a plastic stencil using a black ink pen. The spacing between adjacent points was 2 cm. A photograph was taken of the participant's hand showing the 9 locations for offline coding. The use of a 3 × 3 grid is consistent with many previous studies using this paradigm (e.g., Kang & Longo, 2023; Longo, 2024; Mancini et al., 2011; Medina et al., 2018) and is intended to present stimuli across a wide range of locations on the hand dorsum. No attempt was made to match the distance between stimulus locations to spatial thresholds, which will undoubtedly be much finer than 2 cm.

The stimulus was a von Frey hair producing 26 g of pressure (North Coast Medical, Morgan Hill, CA). On skin trials, the von Frey hair was applied directly onto one of the 9 stimulus locations for approximately 1 sec. On hair trials, the von Frey hair was used to deflect the hair whose base was closest to one of the points, without making any contact with the skin, again for approximately 1 sec. While we aimed to stimulate an individual hair, in many if not most cases this was not possible and multiple hairs were deflected. In most cases, it is likely that terminal hairs were stimulated given that they are larger and more visually apparent. But no systematic effort was made to avoid stimulating vellus hairs. Depending on the orientation of the hair, deflection was generally upwards or in a distal-to-proximal direction.

The task was to indicate where if felt like each stimulus had been applied by using the mouse to position a thin crosshair on a photograph of a hand. The same hand image was used for all participants. The starting location of the crosshair was randomised on each trial to prevent the participant from using their previous response as an anchor. A custom script in MATLAB (MathWorks, Natick, MA) was used to control the experiment, using the Psychtoolbox (Kleiner et al., 2007).

Participants were instructed that if they did not feel a sensation on any given trial that they should click the mouse cursor at the bottom right corner of the screen rather than on the hand image. Such trials were excluded from analyses (Experiment 1: 2.2% of hair trials, .7% of skin trials; Experiment 2: .9% of hair trials, .2% of skin trials).

There were 2 blocks involving with hair stimulation and two involving skin stimulation. The 4 blocks were counterbalanced in an ABBA fashion, with the initial condition counterbalanced across participants. Each block consisted of 27 trials, formed by 3 repetitions of each of the 9 stimulus locations. The order of these 27 trials was pseudorandomised. There were thus 108 trials in total.

Experiment 2. The procedures for the second experiment were similar to Experiment 1 except that stimuli were presented to the left forearm. Before the experiment, a 9 × 3 grid of points was drawn on the dorsal surface of the left forearm using a plastic stencil and a black pen. The 9 rows along the proximo-distal arm axis were separated by 2 cm, while the 3 columns across the medio-lateral arm axis were separated by 1.5 cm. The use of an elongated grid on the forearm was to ensure that stimuli were applied across the entire forearm.

Each block consisted of a single repetition of each of the 27 stimulus locations, again resulting in a total of 108 trials.

1.3. Analysis

Analysis procedures were similar to our recent study of tactile localisation on fingernails (Longo, 2024). Procrustes alignment (Goodall, 1991) was used to put the perceptual map of localization judgments into best-fitting alignment with the actual locations of stimuli. Procrustes alignment involves a geometric transformation of one set of landmarks to place them into best-fitting alignment with another set of homologous landmarks by translating, scaling, and rotating the map. Critically, this transformation preserves the shape of each configuration.

We first used Procrustes alignment to produce a graphic visualization of the average pattern of responses as a perceptual map. These maps are shown below in Fig. 2 for Experiment 1 and in Fig. 4 for Experiment 2. We then used a quantitative measure known as the Procrustes distance to quantify the dissimilarity between each participant's perceptual map and the actual grid of stimulus locations. The Procrustes distance reflects the difference in shape that remains between two maps once they are in Procrustes alignment with each other. For comparison, we calculated a null distribution using simulations of random data. Separate null distributions of one million simulations each were created for Experiments 1 and 2, since the two experiments involved different stimulus distributions. These null distributions allowed us to calculate a p-value for each participant's tactile localisation performance. We further calculated a null distribution for the grand mean Procrustes distance across participants by taking samples of 19 values from the previously described distribution of stimulations. Again, we calculated one million simulations for each null distribution. This allowed us to calculate p-values for the grand average Procrustes distance.

A second type of analysis was based Miller et al. (2018) who quantified localisation ability on tools. In this method, linear regression is used to model how judged location changes as a function of actual stimulus location. If the participant has no ability to localize the stimulus, then on average regression slopes should be centred around 0. In contrast, if the participant has perfect ability to localize, then regression slopes should be centred around 1. The ability of participants to localize at better than chance levels can thus be assessed using a one-sample t-test to compare mean regression slopes to 0. Similarly, deviation from optimal performance can be assessed using a one-sample t-test to compare mean regression slopes to 1.

In Miller et al. (2018) study, performance was assessed only along the one-dimensional length of the held rod. In this study, in contrast, localization was performed in two-dimensional space. Therefore, we conducted separate regression analyses in the proximo-distal (hand/arm length) and medio-lateral (hand/arm width) axes, as in our recent study on the fingernails (Longo, 2024). To operationalize these two limb axes, we used the two-point registration method developed by Bookstein (1991) in which two anatomical landmarks are defined as points (0,0) and (1,0) of a coordinate system, with a second axis defined orthogonal to the first one. For the hand dorsum in Experiment 1, the two reference landmarks were the knuckles of the little and index fingers, consistent with previous studies using this paradigm (Mancini et al., 2011; Margolis & Longo, 2015; S. Medina et al., 2018). For the forearm in Experiment 2, the two reference landmarks were the left and right edges of the arm at the wrist. These landmarks were coded both for the photographs of each participant's actual arm showing the stimulus locations and for the template photographs used for responding. This allowed the locations of stimuli on the participant's actual arm and responses on the image on the monitor to be represented in a commensurate reference frame for analysis.

In each experiment, four linear regressions were performed for each participant, one in each of the two orientations for each of the two types of stimulation (hair vs. skin). Mean regression coefficients were then compared both with 0 (i.e., chance performance) and with 1 (i.e., optimal performance) using one-sample t-tests. Analysis of variance (ANOVA) was used to assess the effects of orientation and stimulation type, using JASP version 0.16.1.

Experimental scripts, raw data, and analysis scripts are available on the Open Science Framework (https://osf.io/tck6s/).

2. Results

2.1. Experiment 1

The results from Experiment 1 are shown in Fig. 1. The top panel show perceptual maps of tactile localization judgments from stimulation of the skin of the hand dorsum (left panel) and from stimulation of hairs (right panel). It is immediately clear from the figure that the nine stimulus locations are placed in the correct relative positions for both types of stimulation. This effect was quantified by calculating the Procrustes distance between each participant's perceptual map and a square grid, which was compared to a null distribution calculated by simulation, as shown in the bottom row of Fig. 1. Significant localization, as index by a Procrustes distance smaller than expected by chance, was found for all 19 participants for both skin stimulation (all p-values <.0001, bottom left panel) and for hair stimulation (all p-values <.0001, bottom centre panel). Grand mean Procrustes distances were compared with a null distribution in which simulated data from 19 participants was generated. Data for both the skin (*M*: .064, *SD*: .061) and the hair (*M*: .081, *SD*: .058) was far lower than any values obtained in simulations (smallest simulated value: .721; bottom right panel). Procrustes distances for hair stimulation was significantly larger than for skin stimulation, $t(18) = 3.01$, $p < .01$, $d_z = .691$. There was a strong correlation across participants between the two stimulation types, $r(17) = .916$, $p < .0001$.

The results from the regression analysis are shown in the left panel of Fig. 2. On the skin, performance was unsurprisingly nearly perfect. Across hand width, the mean regression slope was 1.025 (*SD*: .133), which was significantly higher than 0, $t(18) = 33.65$, $p < .0001$, $d = 7.719$, showing above chance performance, and not significantly different from 1, $t(18) = .815$, $p = .426$, $d = .187$, showing no deviation from optimal performance. Similarly, along hand length, the mean

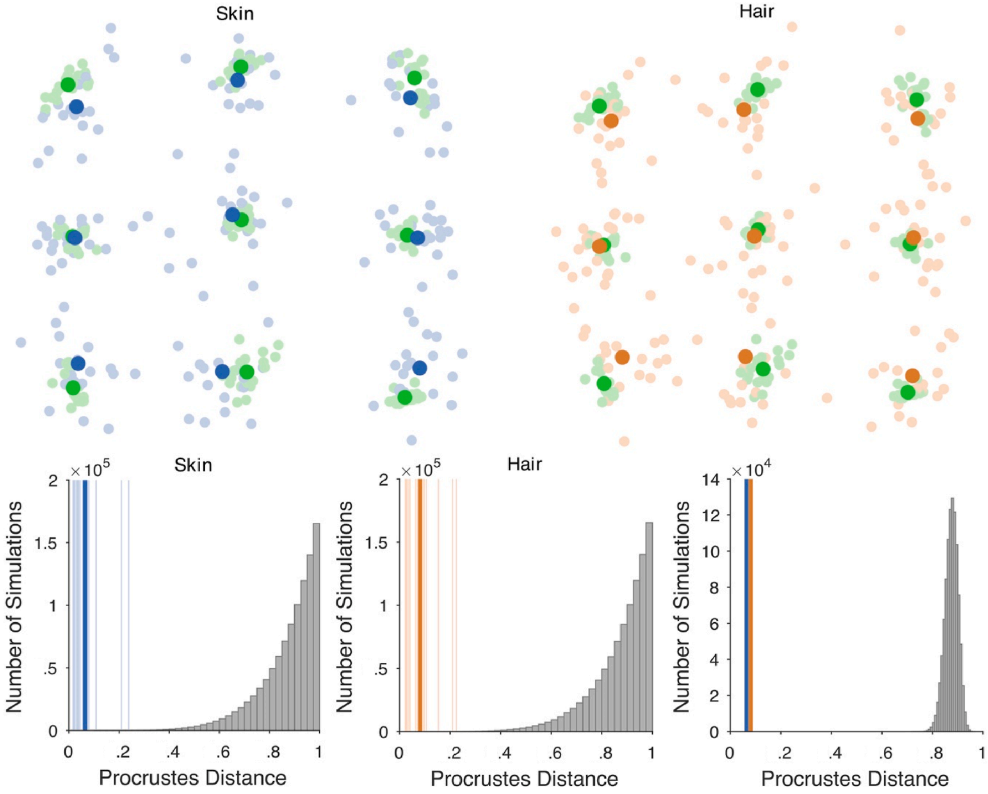

Fig. 1 — Results from Experiment 1. *Top row*: Maps of the nine actual stimulus locations (in green) and judged locations for stimulation of the skin (top left, in blue) and stimulation of hairs (top right, in orange), placed into Procrustes alignment. Dark marks indicate grand means across participants, while lighter marks show mean values for each individual participant. Because Procrustes alignment involves a size normalisation step, distances are in arbitrary units. *Bottom row*: Procrustes distances comparing perceptual maps to square grids for skin stimulation (bottom left, in blue) and hair stimulation (bottom centre, in orange). Thin vertical lines are individual participants, while thick lines are grand means. The grey histograms show a null distribution from simulations of single participants (bottom left and centre) and from simulations of a sample of 19 participants (bottom right).

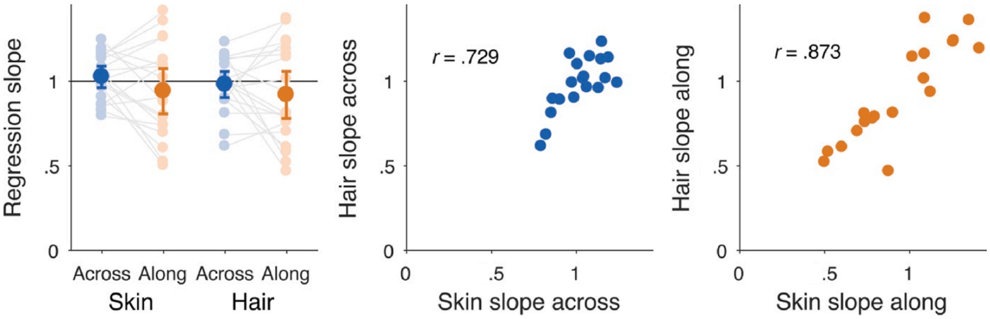

Fig. 2 — Analysis of regression slopes on the hand dorsum in Experiment 1. *Left panel*: Mean slopes regressing judged stimulus location on actual stimulus location in both orientations for stimulation of the skin and of hairs. If participants were unable to localise at all, then on average slopes should equal 0; in contrast, an ideal observer should have a regression slope of 1. The results show near optimal localization performance for both stimulus types. *Centre and right panels*: Scatterplot showing the relation between regression slopes for skin and hair stimulation across hand width (centre panel) and along hand length (right panel). There were clear correlations in both orientations.

regression slope was .941 (*SD*: .277), again significantly greater than 0, $t(18) = 14.80$, $p < .0001$, $d = 3.396$, but not significantly different from 1, $t(18) = -.93$, $p = .364$, $d = .214$.

Results for hair stimulation were very similar. Across hand width, the mean regression slope was .980 (*SD*: .160), which was significantly greater than 0, $t(18) = 26.71$, $p < .0001$, $d = 6.128$, but not significantly different from 1, $t(18) = -.54$, $p = .598$, $d = .123$. Along hand length, the mean regression slope was .919 (*SD*: .288), which was significantly greater than 0, $t(18) = 13.89$, $p < .0001$, $d = 3.186$, but not significantly different from 1, $t(18) = -1.23$, $p = .235$, $d = .282$. Consistent with the analysis of Procrustes distance above, these results show clearly that people are able to precisely localize tactile stimulation of hairs.

A repeated-measures ANOVA on regression slopes showed no main effect of stimulation type, $F(1, 18) = 2.07$, $p = .167$, $\eta^2 = .014$, orientation, $F(1, 18) = 1.65$, $p = .215$, $\eta^2 = .066$, nor an interaction, $F(1, 18) = .39$, $p = .540$, $\eta^2 = .002$.

The centre and right panels of Fig. 2 show correlations between skin and hair stimulation for regression slopes across hand width (centre panel) and along hand length (right panel). There were significant correlations between the two stimulation types both across hand width, $r(17) = .729$, $p < .0005$, and along hand length, $r(17) = .873$, $p < .0001$.

Finally, to assess localisation accuracy in more interpretable units, we calculated for each trial the absolute localisation error in mm. On average, errors were slightly larger for hair stimulation (*M*: 14.9 mm, *SD*: 3.2) than for skin stimulation (*M*: 13.8 mm, *SD*: 3.4), $t(18) = 2.37$, $p < .05$, $d_z = .543$. There was again a strong correlation between error magnitude in the two conditions, $r(17) = .831$, $p < .0001$.

Participants naturally varied in how hairy their hands and forearms were. While this was not assessed quantitatively, it is likely to be associated with the sex of participants. We therefore conducted exploratory analyses including sex as a between-subjects factor for all the main analyses (of Procrustes distance, regression slopes, and absolute error). There were no significant effects of sex and the inclusion of sex had no substantial influence on any other effects.

2.2. *Experiment 2*

The results from Experiment 2 are shown in Fig. 3. The top two panels show perceptual maps of tactile localisation of the skin of the forearm (top panel) and the hair (middle panel). As in Experiment 1, it is visually obvious from the figure that participants can perform the task precisely with both types of stimulation. The bottom row shows Procrustes distances between each participant's perceptual map and a rectangular grid. As in Experiment 1, significant localization as shown by a Procrustes distance smaller than expected by chance, was found for all participants for both skin stimulation (all *p*-values <.0001, bottom left panel) and hair stimulation (all *p*-values <.0001, bottom centre panel). Grand mean Procrustes distances were far lower than in any simulations (smallest simulated value: .895; bottom right panel), both for skin stimulation (*M*: .097, *SD*: .043) and for hair stimulation (*M*: .099, *SD*: .056). There was no significant difference in Procrustes distance between the two stimulation types, $t(18) = .27$, $p = .787$, $d_z = .065$. There was, however, a strong correlation between them, $r(17) = .844$, $p < .0001$.

The results from the regression analysis are shown in Fig. 4. Overall, regression slopes were lower than in Experiment 1, but still quite high. For skin stimulation, the mean regression slope across arm width was .727 (*SD*: .313), which was significantly greater than 0, $t(18) = 10.11$, $p < .0001$, $d = 2.320$, but also significantly less than 1, $t(18) = -3.80$, $p < .002$, $d = .872$. Similarly, along arm length, the mean regression coefficient was .808 (*SD*: .145), significantly greater than 0, $t(18) = 24.25$, $p < .0001$, $d = 5.563$, but significantly less than 1, $t(18) = -5.75$, $p < .0001$, $d = 1.320$.

Similarly, for hair stimulation, the mean regression slope across arm width was .686 (*SD*: .316), significantly greater than 0, $t(18) = 9.47$, $p < .0001$, $d = 2.172$, but significantly less than 1, $t(18) = -4.34$, $p < .0005$, $d = .995$. Along arm length, the mean regression slope was .793 (*SD*: .144), significantly greater than 0, $t(18) = 24.08$, $p < .0001$, $d = 5.524$, but significantly less than 1, $t(18) = -6.27$, $p < .0001$, $d = 1.438$.

A repeated-measures ANOVA showed no significant effect of stimulus type, $F(1, 18) = 3.41$, $p = .081$, $\eta^2 = .006$, of orientation, $F(1, 18) = 1.52$, $p = .234$, $\eta^2 = .073$, or their interaction, $F(1, 18) = 1.03$, $p = .323$, $\eta^2 = .001$.

While there was no significant difference in regression slopes between orientations overall, it is clear from Fig. 4 that there was greater variability across individuals in the across orientation. Indeed, a few participants performed close to chance levels across forearm width. It is worth pointing out that for these participants similarly poor performance was seen for both skin stimulation and hair stimulation. This shows that the difficulties these participants had in this orientation were not linked to any specific form of stimulation.

Finally, in terms of absolute localisation error, errors did not differ significantly between hair stimulation (*M*: 24.2 mm, *SD*: 7.1) than for skin stimulation (*M*: 23.9 mm, *SD*: 6.9), $t(18) = .88$, $p = .390$, $d_z = .202$. There was again a strong correlation between error magnitude in the two conditions, $r(17) = .967$, $p < .0001$.

As in Experiment 1, when sex was included as a between-subject factor there were no significant effects of sex and no substantive change in any other effects.

3. Discussion

The results of this study demonstrate that people can precisely localise tactile stimulation of hair. Localisation performance for hair stimulation was clearly above chance levels, and not appreciably lower than performance following stimulation of the skin itself. Similar results were found for stimulation of hairs on the hand dorsum (Experiment 1) and the forearm (Experiment 2).

Classic findings of the sensory physiology of hairs showed strong responses to gentle strokes (Zotterman, 1939). This led to the suggestion that hair follicle receptors act as movement detectors (Brown & Iggo, 1967). Indeed, a recent study used electrostatic stimulation to produce patterns of movement evoked by hair erection on the forearm, showing that human

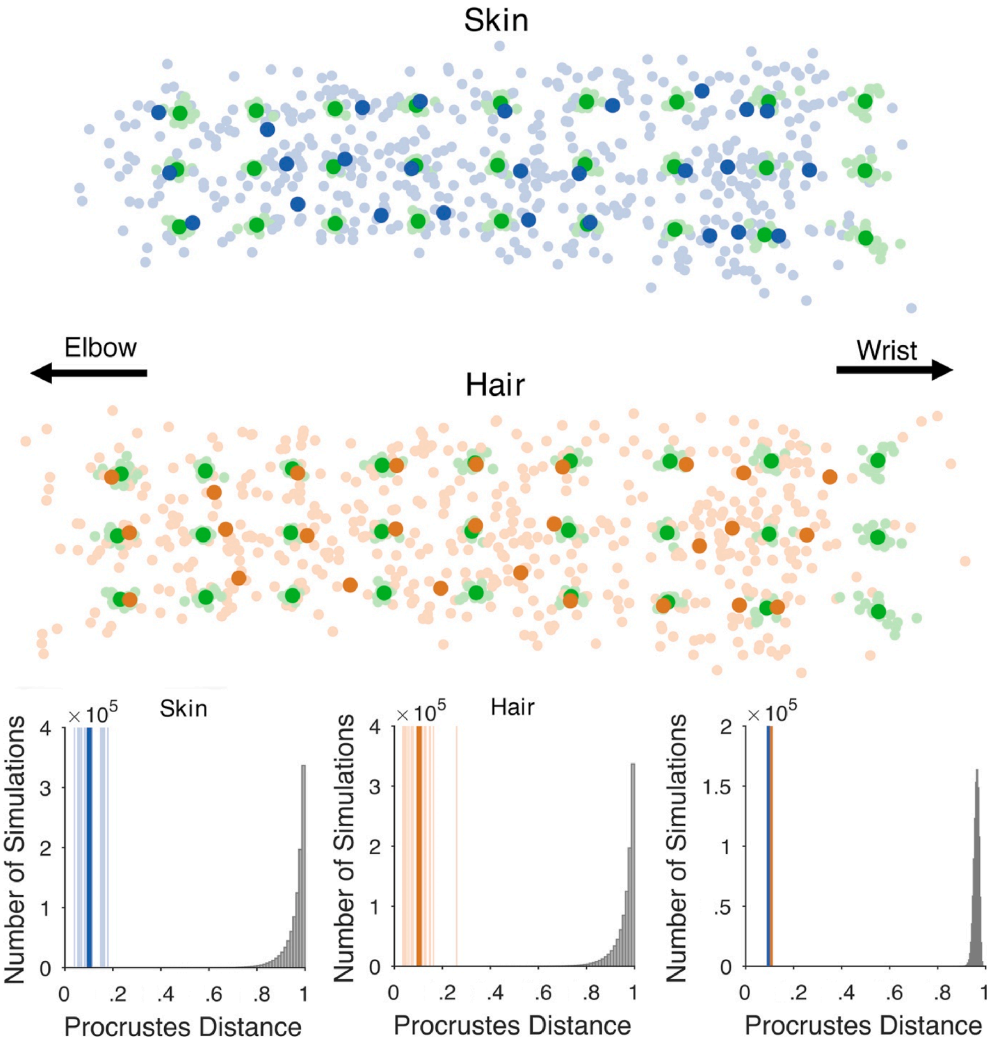

Fig. 3 – Results from Experiment 2. *Top row*: Maps of the 27 actual stimulus locations (in green) and judged locations for stimulation of the skin (top, in blue) and stimulation of hairs (centre, in orange), placed into Procrustes alignment. Dark marks indicate grand means across participants, while lighter marks show mean values for each individual participant. *Bottom row*: Procrustes distances comparing perceptual maps to square grids for skin stimulation (bottom left, in blue) and hair stimulation (bottom centre, in orange). Thin vertical lines are individual participants, while thick lines are grand means. The grey histograms show a null distribution from simulations of single participants (bottom left and centre) and from simulations of a sample of 19 participants (bottom right).

participants could classify direction of motion at high levels of accuracy (Bouzbib et al., in press). More recently, the discovery of unmyelinated CT afferents in human hairy skin which respond maximally to moving stimuli (Löken et al., 2009; Morrison et al., 2011) has led to hair stimulation being interpreted as related to affective – rather than discriminative – touch (McGlone et al., 2014). Such research has shown a central role of hair in tactile movement perception and interpersonal, affective touch, which has been a major focus of recent research (e.g., Fotopoulou et al., 2022; Morrison & Croy, 2021; Schirmer et al., 2023; Xu et al., 2025), although a recent study failed to find any close relation between hair follicle density and affective touch (Jönsson et al., 2017). Another recent study found that stimulation of vellus hairs on the face – but not on the arm – elicited sensations of itch (Fukuoka et al., 2013). The present results provide evidence that human hairs can also support spatial, discriminative perception of punctate tactile stimuli. This is consistent with research mentioned in the Introduction showing widespread discriminative functions of sensory hairs across the animal kingdom (Boublil et al., 2021).

Mancini et al. (2011) compared tactile localisation performance for stimuli activating Aβ (innocuous touch), Aδ (pinprick pain), and C fibers (nonpainful heat). Based on similar patterns of mislocalisation across stimulation types, these authors argued that tactile localisation relies on a supramodal representation of the skin, which is used irrespective of the nature of the stimulation. The present results are consistent with this interpretation. Not only were broadly similar levels of spatial precision seen for localisation of touch applied to hairs and to the skin, but precision was strongly

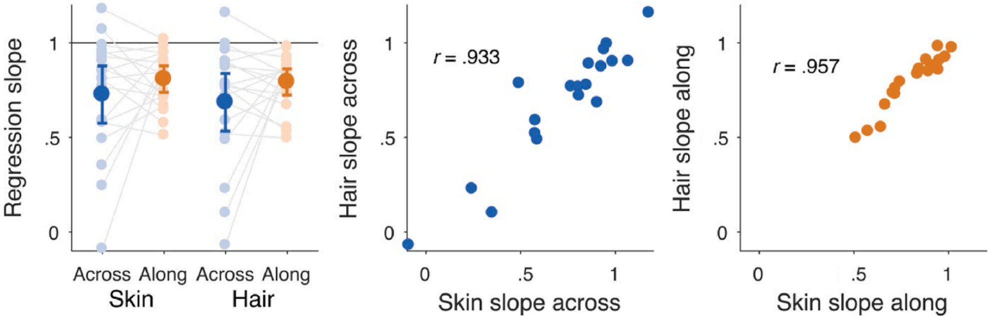

Fig. 4 – Analysis of regression slopes on the forearm in Experiment 2. *Left panel*: Mean slopes regressing judged stimulus location on actual stimulus location in both orientations for stimulation of the skin and of hairs. If participants were unable to localise at all, then on average slopes should equal 0; in contrast, an ideal observer should have a regression slope of 1. *Centre and right panels*: Scatterplot showing the relation between regression slopes for skin and hair stimulation across hand width (centre panel) and along hand length (right panel). There were clear correlations in both orientations.

correlated across participants for the two types of stimulation. At the same time, given the highly similar results in the two modalities and the strong correlations between them, it is also possible that both types of stimulation result in activation of the same receptors in the skin. This interpretation is consistent with physiological findings that receptors sensitive to hair deflection can also be activated by stimulation of the skin (Vallbo et al., 1995).

The ability to localise touch from stimulation of hairs may be related to a wider class of remote sensing, in which people are able to obtain tactile information from stimulation which is spatially removed from the actual size of the mechanosensory receptors. The most familiar example of this is in tool use, such as the use of canes by blind people (Descartes, 1637; Gibson, 1966; James, 1890; Lotze, 1885). This ability has recently been studied by Miller et al. (2018, 2019) who have shown elegantly that people can judge precisely where along the length of a wielder rod a tactile stimulus was applied. Another example is the recent demonstration of precise localisation of tactile stimuli on the human fingernail (Longo, 2024). Similarly, people are able to discriminate the roughness of stimuli applied to the fingertips even when the fingertips themselves are anaesthetised using the wider pattern of vibrations produced at other locations on the hand and arm (Delhaye et al., 2012; Libouton et al., 2012). There also appears to be some ability to perceive spatially using the teeth. This appears true even for prosthetic teeth following tooth extraction, an ability known as *osseoperception* (Jacobs & Van Steenberghe, 2006; Klineberg & Murray, 1999). In each of these cases, spatial information is obtained about stimuli distant from the location of the peripheral mechanoreceptors, consistent with the argument that Gibson (1966, p. 100) made over 50 years ago that “The tactual system is not, then, strictly a ‘proximity sense’ as traditionally assumed, for the appendages of the skin protrude into the environment.”

The present study showed a precise ability to localise hair stimulation, but did not measure subjective experiences of what hair stimulation feels like. Trulsson and Essick (2010) used microneurography to electrically stimulate individual afferent fibres sensitive to hair deflection on the face. This produced experiences of “tapping of the hair” (p. 1745). It will be interesting in future research to investigate how localisation relates to specific experiences of hair stimulation. It is possible that different types of hair stimulation (e.g., displacement versus tugging) might produce different types of subjective experiences and be associated with different levels of precision of localisation.

The rich perceptual sensitivity of whiskers in rodents is due in large part to the use of active whisking movements (Knutsen et al., 2006; Mehta et al., 2007; Sofroniew & Svoboda, 2015). This is analogous to the way in which active movements of the hand dramatically enhance the perceptual power of human haptic exploration compared to passive touch (Gibson, 1966; Jones, 2018; Katz, 1925; Lederman & Klatzky, 1987). The present results, however, show that rich spatial information can be obtained from purely passive stimulation of hairs. This shows that active movements of hairs are not necessary to obtain spatial information, at least in some cases.

It is likely that the skin stimulation in this study resulted in the activation of a larger number of mechanoreceptors than hair stimulation. In addition, when the skin was stimulated some hairs will also have been displaced. Given this, it is noteworthy that localisation performance was only very modestly better for skin stimulation than for hair stimulation. Differences between the two stimulation types were small, were only seen on the hand (EXP 1) and not on the forearm (EXP 2), and did not appear for all measures. There were also strong correlations across individuals between performance in the two conditions, which showed a striking level of similarity.

In the present study, no systematic attempt was made to distinguish the specific types of hair stimulated (e.g., vellus versus terminal). Given that terminal hairs are larger and darker, and thus easier to see, they were presumably overrepresented in our study compared to vellus hairs. It would be interesting in future research to study more systematically whether each of these types of hair can support the precise tactile localisation we describe. Interestingly, large beard hairs appear to be organised differently, with each individual hair linked to a unique afferent fibre (Trulsson & Essick, 2010), which could potentially support even more precise localisation. Another important limitation of the present study is that more than one hair may have been stimulated on each trial, given that in some cases the density of hairs was such that it was not possible to stimulate only one. This might enhance performance by increasing the total amount of stimulation, or reduce performance by making the stimulation feel more diffuse. It is relevant here to note, as mentioned above, that individual afferents in the hand and forearm are linked to groups of 20–25 hairs (Corniani & Saal, 2020; Vallbo et al., 1995). Thus, it is possible that simultaneous stimulation of a group of nearby hairs may nevertheless activate only a single peripheral afferent fibre.

The human hand includes a rich array of sensory receptors, subserving an extraordinary range of perceptual abilities (Longo, 2025). While most research has understandably focused on the (hairless) glabrous skin of the palmar hand surface, the present results highlight the rich sensory information that can be obtained from human hair.

CRediT authorship contribution statement

Matthew R. Longo: Writing – original draft, Visualization, Supervision, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Cleo Sakka:** Writing – review & editing, Investigation, Conceptualization.

Scientific transparency statement

DATA: All raw and processed data supporting this research are publicly available: https://osf.io/tck6s/

CODE: All analysis code supporting this research is publicly available: https://osf.io/tck6s/

MATERIALS: All study materials supporting this research are publicly available: https://osf.io/tck6s/

DESIGN: This article reports, for all studies, how the author (s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.

PRE-REGISTRATION: No part of the study procedures was pre-registered in a time-stamped, institutional registry prior to the research being conducted. No part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted.

For full details, see the *Scientific Transparency Report* in the supplementary data to the online version of this article.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2025.11.002.

REFERENCES

Ackerley, R., Backlund Wasling, H., Liljencrantz, J., Olausson, H., Johnson, R. D., & Wessberg, J. (2014). Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. *Journal of Neuroscience, 34*(8), 2879–2883. https://doi.org/10.1523/JNEUROSCI.2847-13.2014

Adrian, E. D. (1941). Afferent discharges to the cerebral cortex from peripheral sense organs. *Journal of Physiology, 100*(2), 159–191. https://doi.org/10.1113/jphysiol.1941.sp003932

Agramunt, J., Parke, B., Mena, S., Ubels, V., Jimenez, F., Williams, G., Rhodes, A. D., Limbu, S., Hexter, M., Knight, L., Hashemi, P., Kozlov, A. S., & Higgins, C. A. (2023). Mechanical stimulation of human hair follicle outer root sheath cultures activates adjacent sensory neurons. *Science Advances, 9*(43). https://doi.org/10.1126/sciadv.adh3273. eadh3273.

Ahl, A. S. (1982). Evidence of use of vibrissae in swimming in *Sigmodon fulviventer*. *Animal Behaviour, 30*(4), 1203–1206. https://doi.org/10.1016/S0003-3472(82)80211-X

Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press.

Boublil, B. L., Diebold, C. A., & Moss, C. F. (2021). Mechanosensory hairs and hair-like structures in the animal kingdom: Specializations and shared functions serve to inspire technology applications. *Sensors, 21*(19), 6375. https://doi.org/10.3390/s21196375

Bouzbib, E., Donkov, S., Elizondo, S., Irisarri, J., Aldea, M., Ezcurdia, I., Iriarte, N., & Marzo, A. (in press). ElectroCaresses: Contactless apparent motion on the forearm using electrostatic piloerection. IEEE Transactions on Haptics, 1–11. https://doi.org/10.1109/TOH.2025.3579134.

Brecht, M., Preilowski, B., & Merzenich, M. M. (1997). Functional architecture of the mystacial vibrissae. *Behavioural Brain Research, 84*(1–2), 81–97. https://doi.org/10.1016/S0166-4328(97)83328-1

Brown, A. G., & Iggo, A. (1967). A quantitative study of cutaneous receptors and afferent fibres in the cat and rabbit. *Journal of Physiology, 193*(3), 707–733. https://doi.org/10.1113/jphysiol.1967.sp008390

Buffoli, B., Rinaldi, F., Labanca, M., Sorbellini, E., Trink, A., Guanziroli, E., Rezzani, R., & Rodella, L. F. (2014). The human hair: From anatomy to physiology. *International Journal of Dermatology, 53*(3), 331–341. https://doi.org/10.1111/ijd.12362

Carvell, G. E., & Simons, D. J. (1990). Biometric analyses of vibrissal tactile discrimination in the rat. *Journal of Neuroscience, 10*(8), 2638–2648. https://doi.org/10.1523/JNEUROSCI.10-08-02638.1990

Corniani, G., & Saal, H. P. (2020). Tactile innervation densities across the whole body. *Journal of Neurophysiology, 124*(4), 1229–1240. https://doi.org/10.1152/jn.00313.2020

Delhaye, B., Hayward, V., Lefèvre, P., & Thonnard, J.-L. (2012). Texture-induced vibrations in the forearm during tactile exploration. *Frontiers in Behavioral Neuroscience, 6*, 37. https://doi.org/10.3389/fnbeh.2012.00037

Descartes, R. (1637). La dioptrique [Optics].

Diamond, M. E., Von Heimendahl, M., Knutsen, P. M., Kleinfeld, D., & Ahissar, E. (2008). 'Where' and 'what' in the whisker sensorimotor system. *Nature Reviews Neuroscience, 9*(8), 601–612. https://doi.org/10.1038/nrn2411

Drake, S. E., Crish, S. D., George, J. C., Stimmelmayr, R., & Thewissen, J. G. M. (2015). Sensory hairs in the bowhead whale, *Balaena mysticetus* (Cetacea, Mammalia). *Anatomical Record, 298*(7), 1327–1335. https://doi.org/10.1002/ar.23163

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods, 39*, 175–191. https://doi.org/10.3758/BF03193146

Fotopoulou, A., von Mohr, M., & Krahé, C. (2022). Affective regulation through touch: Homeostatic and allostatic mechanisms. *Current Opinion in Behavioral Sciences, 43*, 80–87. https://doi.org/10.1016/j.cobeha.2021.08.008

Fraser, P. J. (1977). Cercal ablation modifies tethered flight behaviour of cockroach. *Nature, 268*(5620), 523–524. https://doi.org/10.1038/268523a0

Fukuoka, M., Miyachi, Y., & Ikoma, A. (2013). Mechanically evoked itch in humans. *Pain, 154*(6), 897–904. https://doi.org/10.1016/j.pain.2013.02.021

Ghitani, N., Barik, A., Szczot, M., Thompson, J. H., Li, C., Le Pichon, C. E., Krashes, M. J., & Chesler, A. T. (2017). Specialized mechanosensory nociceptors mediating rapid responses to hair pull. *Neuron, 95*(4), 944–954.e4. https://doi.org/10.1016/j.neuron.2017.07.024

Gibson, J. J. (1966). *The senses considered as perceptual systems.* Houghton Mifflin.

Goodall, C. (1991). Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society B, 53*, 285–321. https://doi.org/10.1111/j.2517-6161.1991.tb01825.x

Grunwald, M., Pasatu, W. P. M., Spille, J., Haensel, R., Stieler, J., Holzer, M., Ziemer, M., Butz, K. H. G., Martin, S., Mueller, S. M., & Morawski, M. (2025). Number of facial hair corresponds to frequency of spontaneous face-touch in humans. *Advanced Biology, 9*(2), Article 2400243. https://doi.org/10.1002/adbi.202400243

Guić-Robles, E., Valdivieso, C., & Guajardo, G. (1989). Rats can learn a roughness discrimination using only their vibrissal system. *Behavioural Brain Research, 31*(3), 285–289. https://doi.org/10.1016/0166-4328(89)90011-9

Halligan, P. W., Hunt, M., Marshall, J. C., & Wade, D. T. (1995). Sensory detection without localization. *Neurocase, 1*, 259–266. https://doi.org/10.1080/13554799508402370

Handler, A., & Ginty, D. D. (2021). The mechanosensory neurons of touch and their mechanisms of activation. *Nature Reviews Neuroscience, 22*, 521–537. https://doi.org/10.1038/s41583-021-00489-x

Harvey, M. A., Bermejo, R., & Zeigler, H. P. (2001). Discriminative whisking in the head-fixed rat: Optoelectronic monitoring during tactile detection and discrimination tasks. *Somatosensory & Motor Research, 18*(3), 211–222. https://doi.org/10.1080/01421590120072204

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain, 34*, 102–254. https://doi.org/10.1093/brain/34.2-3.102

Iggo, A. (1960). Cutaneous mechanoreceptors with afferent C fibres. *Journal of Physiology, 152*(2), 337–353. https://doi.org/10.1113/jphysiol.1960.sp006491

Jönsson, E. H., Bendas, J., Weidner, K., Wessberg, J., Olausson, H., Wasling, H. B., & Croy, I. (2017). The relation between human hair follicle density and touch perception. *Scientific Reports, 7*(1), 2499. https://doi.org/10.1038/s41598-017-02308-9

Jacobs, R., & Van Steenberghe, D. (2006). From osseoperception to implant-mediated sensory-motor interactions and related clinical implications. *Journal of Oral Rehabilitation, 33*(4), 282–292. https://doi.org/10.1111/j.1365-2842.2006.01621.x

James, W. (1890). *The principles of psychology.* Dover.

Jenkinson, E. W., & Glickstein, M. (2000). Whiskers, barrels, and cortical efferent pathways in gap crossing by rats. *Journal of Neurophysiology, 84*(4), 1781–1789. https://doi.org/10.1152/jn.2000.84.4.1781

Jones, L. A. (2018). *Haptics.* MIT Press.

Kaas, J. H., Nelson, R. J., Sur, M., Dykes, R. W., & Merzenich, M. M. (1984). The somatotopic organization of the ventroposterior thalamus of the squirrel monkey, *Saimiri sciureus*. *Journal of Comparative Neurology, 226*(1), 111–140. https://doi.org/10.1002/cne.902260109

Kang, W., & Longo, M. R. (2023). Tactile localization on stretched skin. *Journal of Experimental Psychology: Human Perception and Performance, 49*(8), 1175–1179. https://doi.org/10.1037/xhp0001142

Katz, D. (1925). *The world of touch [L.E. Krueger, Trans.].* Erlbaum.

Kleiner, M., Brainard, D. H., & Pelli, D. (2007). What's new in psychtoolbox-3? *Perception, 36. ECVP 2007 Abstract Supplement)*(14.

Klineberg, I., & Murray, G. (1999). Osseoperception: Sensory function and proprioception. *Advances in Dental Research, 13*, 120–129. https://doi.org/10.1177/08959374990130010101

Knutsen, P. M., & Ahissar, E. (2009). Orthogonal coding of object location. *Trends in Neurosciences, 32*(2), 101–109. https://doi.org/10.1016/j.tins.2008.10.002

Knutsen, P. M., Pietr, M., & Ahissar, E. (2006). Haptic object localization in the vibrissal system: Behavior and performance. *Journal of Neuroscience, 26*(33), 8451–8464. https://doi.org/10.1523/JNEUROSCI.1516-06.2006

Krupa, D. J., Matell, M. S., Brisben, A. J., Oliveira, L. M., & Nicolelis, M. A. L. (2001). Behavioral properties of the trigeminal somatosensory system in rats performing whisker-dependent tactile discriminations. *Journal of Neuroscience, 21*(15), 5752–5763. https://doi.org/10.1523/JNEUROSCI.21-15-05752.2001

Kumazawa, T., & Perl, E. R. (1977). Primate cutaneous sensory units with unmyelinated (C) afferent fibers. *Journal of Neurophysiology, 40*(6), 1325–1338. https://doi.org/10.1152/jn.1977.40.6.1325

Löken, L. S., Wessberg, J., Morrison, I., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience, 12*(5), 547–548. https://doi.org/10.1038/nn.2312

Lechner, S. G., & Lewin, G. R. (2013). Hairy sensation. *Physiology, 28*(3), 142–150. https://doi.org/10.1152/physiol.00059.2012

Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition. *Cognitive Psychology, 19*, 342–368. https://doi.org/10.1016/0010-0285(87)90008-9

Li, L., & Ginty, D. D. (2014). The structure and organization of lanceolate mechanosensory complexes at mouse hair follicles. *eLife, 3*, Article e01901. https://doi.org/10.7554/eLife.01901

Li, L., Rutlin, M., Abraira, V. E., Cassidy, C., Kus, L., Gong, S., Jankowski, M. P., Luo, W., Heintz, N., Koerber, H. R., Woodbury, C. J., & Ginty, D. D. (2011). The functional organization of cutaneous low-threshold mechanosensory neurons. *Cell, 147*(7), 1615–1627. https://doi.org/10.1016/j.cell.2011.11.027

Libouton, X., Barbier, O., Berger, Y., Plaghki, L., & Thonnard, J.-L. (2012). Tactile roughness discrimination of the finger pad relies primarily on vibration sensitive afferents not necessarily located in the hand. *Behavioural Brain Research, 229*(1), 273–279. https://doi.org/10.1016/j.bbr.2012.01.018

Longo, M. R. (2024). Precise tactile localization on the human fingernail. *Proceedings of the Royal Society B, 291*, Article 20241200. https://doi.org/10.1098/rspb.2024.1200

Longo, M. R. (2025). *The invisible hand: Neurocognitive mechanisms of human hand function.* MIT Press.

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia, 48*, 655–668. https://doi.org/10.1016/j.neuropsychologia.2009.08.022

Longo, M. R., Mancini, F., & Haggard, P. (2015). Implicit body representations and tactile spatial remapping. *Acta Psychologica, 160*, 77–87. https://doi.org/10.1016/j.actpsy.2015.07.002

Lotze, H. (1885). *Microcosmus: An essay concerning man and his relation to the world [E. Hamilton & E.E. Constance Jones, Trans.].* T&T Clark.

Mancini, F., Longo, M. R., Iannetti, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. *Neuropsychologia, 49*, 1194–1201. https://doi.org/10.1016/j.neuropsychologia.2010.12.040

Margolis, A. N., & Longo, M. R. (2015). Visual detail about the body modulates tactile localisation biases. *Experimental Brain*

Research, 233, 351–358. https://doi.org/10.1007/s00221-014-4118-3

McGlone, F., Wessberg, J., & Olausson, H. (2014). Discriminative and affective touch: Sensing and feeling. *Neuron, 82*(4), 737–755. https://doi.org/10.1016/j.neuron.2014.05.001

Medina, J., & Coslett, H. B. (2010). From maps to form to space: Touch and the body schema. *Neuropsychologia, 48*(3), 645–654. https://doi.org/10.1016/j.neuropsychologia.2009.08.017

Medina, S., Tamè, L., & Longo, M. R. (2018). Tactile localization biases are modulated by gaze direction. *Experimental Brain Research, 236*, 31–42. https://doi.org/10.1007/s00221-017-5105-2

Mehta, S. B., Whitmer, D., Figueroa, R., Williams, B. A., & Kleinfeld, D. (2007). Active spatial perception in the vibrissa scanning sensorimotor system. *Plos Biology, 5*(2), e15. https://doi.org/10.1371/journal.pbio.0050015

Miller, L. E., Fabio, C., Ravenda, V., Bahmad, S., Koun, E., Salemme, R., Luauté, J., Bolognini, N., Hayward, V., & Farnè, A. (2019). Somatosensory cortex efficiently processes touch located beyond the body. *Current Biology, 29*, 4276–4283. https://doi.org/10.1016/j.cub.2019.10.043

Miller, L. E., Montroni, L., Koun, E., Salemme, R., Hayward, V., & Farnè, A. (2018). Sensing with tools extends somatosensory processing beyond the body. *Nature, 561*, 239–242. https://doi.org/10.1038/s41586-018-0460-0

Morrison, I., Bjornsdotter, M., & Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. *Journal of Neuroscience, 31*(26), 9554–9562. https://doi.org/10.1523/JNEUROSCI.0397-11.2011

Morrison, I., & Croy, I. (2021). The science of social and affective touch. *Neuroscience, 464*, 1–2. https://doi.org/10.1016/j.neuroscience.2021.03.013

Mountcastle, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *Journal of Neurophysiology, 20*(4), 408–434. https://doi.org/10.1152/jn.1957.20.4.408

Mountcastle, V. B., Davies, P. W., & Berman, A. L. (1957). Response properties of neurons of cat's somatic sensory cortex to peripheral stimuli. *Journal of Neurophysiology, 20*(4), 374–407. https://doi.org/10.1152/jn.1957.20.4.374

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Pammer, L., O'Connor, D. H., Hires, S. A., Clack, N. G., Huber, D., Myers, E. W., & Svoboda, K. (2013). The mechanical variables underlying object localization along the axis of the whisker. *Journal of Neuroscience, 33*(16), 6726–6741. https://doi.org/10.1523/JNEUROSCI.4316-12.2013

Polley, D., Rickert, J., & Frostig, R. (2005). Whisker-based discrimination of object orientation determined with a rapid training paradigm. *Neurobiology of Learning and Memory, 83*(2), 134–142. https://doi.org/10.1016/j.nlm.2004.10.005

Reep, R. L., Marshall, C. D., & Stoll, M. L. (2002). Tactile hairs on the postcranial body in Florida manatees: A mammalian lateral line? *Brain, Behavior and Evolution, 59*(3), 141–154. https://doi.org/10.1159/000064161

Robinson, C. J., & Burton, H. (1980). Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis*. *Journal of Comparative Neurology, 192*(1), 69–92. https://doi.org/10.1002/cne.901920105

Rowe, T. B., Macrini, T. E., & Luo, Z.-X. (2011). Fossil evidence on origin of the mammalian brain. *Science, 332*, 955–957. https://doi.org/10.1126/science.1203117

Sandel, A. A. (2013). Hair density and body mass in mammals and the evolution of human hairlessness. *American Journal of Physical Anthropology, 152*(1), 145–150. https://doi.org/10.1002/ajpa.22333

Schirmer, A., Croy, I., & Ackerley, R. (2023). What are C-tactile afferents and how do they relate to “affective touch”. *Neuroscience and Biobehavioral Reviews, 151*, Article 105236. https://doi.org/10.1016/j.neubiorev.2023.105236

Shuler, M. G., Krupa, D. J., & Nicolelis. (2002). Integration of bilateral whisker stimuli in rats: Role of the whisker barrel cortices. *Cerebral Cortex, 12*(1), 86–97. https://doi.org/10.1093/cercor/12.1.86

Sofroniew, N. J., & Svoboda, K. (2015). Whisking. *Current Biology, 25*(4), R137–R140. https://doi.org/10.1016/j.cub.2015.01.008

Sterbing-D’Angelo, S., Chadha, M., Chiu, C., Falk, B., Xian, W., Barcelo, J., Zook, J. M., & Moss, C. F. (2011). Bat wing sensors support flight control. *Proceedings of the National Academy of Sciences, 108*(27), 11291–11296. https://doi.org/10.1073/pnas.1018740108

Strick, P. L., & Preston, J. B. (1978). Sorting of somatosensory afferent information in primate motor cortex. *Brain Research, 156*(2), 364–368. https://doi.org/10.1016/0006-8993(78)90520-6

Szabo, G. (1967). The regional anatomy of the human integument with special reference to the distribution of hair follicles, sweat glands and melanocytes. *Philosophical Transactions of the Royal Society of London B, 252*(779), 447–485. https://doi.org/10.1098/rstb.1967.0029

Tanji, J., & Wise, S. P. (1981). Submodality distribution in sensorimotor cortex of the unanesthetized monkey. *Journal of Neurophysiology, 45*(3), 467–481. https://doi.org/10.1152/jn.1981.45.3.467

Tautz, J., Masters, W. M., Aicher, B., & Markl, H. (1981). A new type of water vibration receptor on the crayfish antenna. *Journal of Comparative Physiology, 44*, 533–541. https://doi.org/10.1007/BF01326838

Trulsson, M., & Essick, G. K. (2010). Sensations evoked by microstimulation of single mechanoreceptive afferents innervating the human face and mouth. *Journal of Neurophysiology, 103*(4), 1741–1747. https://doi.org/10.1152/jn.01146.2009

Tuthill, J. C., & Wilson, R. I. (2016). Mechanosensation and adaptive motor control in insects. *Current Biology, 26*(20), R1022–R1038. https://doi.org/10.1016/j.cub.2016.06.070

Vallbo, Å. B., Olausson, H., & Wessberg, J. (1999). Unmyelinated afferents constitute a second system coding tactile stimuli of the human hairy skin. *Journal of Neurophysiology, 81*(6), 2753–2763. https://doi.org/10.1152/jn.1999.81.6.2753

Vallbo, Å. B., Olausson, H., Wessberg, J., & Kakuda, N. (1995). Receptive field characteristics of tactile units with myelinated afferents in hairy skin of human subjects. *Journal of Physiology, 483*(3), 783–795. https://doi.org/10.1113/jphysiol.1995.sp020622

Vincent, S. B. (1912). The function of the vibrissae in the behavior of the white rat. *Behavior Monographs, 1*, 1–81.

Weis-Fogh, T. (1949). An aerodynamic sense organ stimulating and regulating flight in locusts. *Nature, 164*(4177), 873–874. https://doi.org/10.1038/164873a0

Xu, S., Hauser, S. C., Nagi, S. S., Jablonski, J. A., Rezaei, M., Jarocka, E., Marshall, A. G., Olausson, H., McIntyre, S., & Gerling, G. J. (2025). Mechanoreceptive Aβ primary afferents discriminate naturalistic social touch inputs at a functionally relevant time scale. *IEEE Transactions on Affective Computing, 16*(1), 346–359. https://doi.org/10.1109/TAFFC.2024.3435060

Yamamoto, S., Sugihara, S., & Kuru, M. (1956). Microelectrode studies on sensory afferents in the posterior funiculus of cat. *Japanese Journal of Physiology, 6*, 68–85. https://doi.org/10.2170/jjphysiol.6.68

Zotterman, Y. (1939). Touch, pain and tickling: An electro-physiological investigation on cutaneous sensory nerves. *Journal of Physiology, 95*(1), 1–28. https://doi.org/10.1113/jphysiol.1939.sp003707