RUNNING HEAD: Tactile Localisation on Fingernails

Precise tactile localisation on the human fingernail

Matthew R. Longo
School of Psychological Sciences, Birkbeck, University of London

Address correspondence to:
Matthew Longo
School of Psychological Sciences
Birkbeck, University of London
Malet Street, London WC1E 7HX
United Kingdom
m.longo@bbk.ac.uk

Abstract

Fingernails are specialised features of the primate hand which are believed to contribute to manual dexterity. The sensorimotor functions of fingernails, however, remain poorly understood. This study investigated the ability of humans to precisely localise touches applied to the fingernail plate. Nine different locations on the fingernail were touched and participants judged the location by clicking a mouse cursor on a photograph of their finger. Performance in this condition was compared to stimuli applied to the skin of the fingertip. The results showed that participants are able to localise touch on the fingernails at substantial higher than chance levels. Moreover, the precision of this ability is not appreciably lower than that on the fingertips. These results show that the fingernail is a highly sensitive sensory organ which is capable to providing rich spatial information about tactile stimuli.

While most mammals have claws on each digit, a characteristic feature of primates is the presence instead of nails [1,2], flattened plates of alpha-keratin which cover the distal extremity of the dorsal surface of digits. Claws, hooves, and nails are homologous structures, which are differentiated developmentally by different patterns of growth [3] and gene expression [4]. The replacement of claws by nails is believed to be linked to the evolutionary emergence of high levels of manual dexterity in primates. For example, fossils of early primates such as the 56-million year-old *Carpolestes simpsoni* show that the emergence of a nail on the thumb co-occurred with other skeletal features linked to manual dexterity, such as the saddle joint at the base of the thumb [5]. Conversely, where claws have re-emerged in primates, it is generally in species with conspicuously poor manual dexterity, such as marmosets [3,6]. The relation between fingernails and manual function is supported by research in humans showing that nail disease is linked with impaired manual dexterity, including in autoimmune conditions such as nail psoriasis [7], fungal infections such as onychomycosis [8], following traumatic injury [9,10], and in congenital fingernail malformation [11]. Nevertheless, the role of fingernails in sensorimotor function remains poorly understood.

There are several reasons why fingernails might be advantageous for sensorimotor function. One possibility is simply that claws would get in the way when making pulp-to-pulp precision grips or power grips used to securely hold objects [12], whereas nails remain conveniently out of the way. Another possibility, which has traditionally been emphasised, is that the fingernail provides a hard supporting background which enhances tactile sensitivity on the skin of the fingertip and helps to keep the fingertips from slipping when handling small objects [13,14]. For example, moistening the fingernails, which reduces their rigidity, reduces perceptual ability to discriminate forces applied to the fingertip [15]. On this view, the fingernails are largely passive support structures, which serve to enhance the sensorimotor functions of the fingertips.

An alternative view, however, comes from experimental psychology, in which some authors have suggested that the fingernails themselves can have active sensory functions. For example, David Katz [16] in his classic studies of tactile texture discrimination noted that most texture differences could be recognised even when the objects were touched only with the fingernails. Similarly, James Gibson [17] emphasised that many tactile sensations can be driven by the fingernail, an ability which he groups with a wider class of remote sensing by non-skin elements such as claws, hooves, horns, hairs, and tools:

> “The tactual system is not, then, strictly a "proximity sense" as traditionally assumed, for the appendages of the skin protrude into the environment. The long-horned animal gets information at some distance from the skin; the man has only to scrape a surface with his fingernail to realize that he is aware of what happens at the end of the nail, not at the root, where the mechanoreceptive neurons are and where the sensations should theoretically be felt. The capacity of vibrissae, hairs, claws, and horns to feel things at a distance is not different in principle from the ability of a man to use a cane or probe to detect the mechanical encounters at the end of the artificial appendage to his hand.” (pg. 100)

Despite this long-standing awareness of the tactile role of the fingernails, little research has investigated these abilities. Neither Katz [16] nor Gibson [17] provides any quantitative data on the tactile abilities of the fingernails. Remarkably, to my knowledge only one study has quantified tactile sensitivity for stimuli delivered directly to the fingernail. Seah and colleagues [18] measured tactile pressure detection thresholds on the fingernails using von Frey hairs and two-point discrimination thresholds for both static and moving stimuli. While static discrimination thresholds were about twice as high on the fingernail as on the fingertip, participants were able to discriminate whether they were touched by one stimulus or two on the fingernail. Indeed, for moving stimuli that slid along the length of the finger, discrimination thresholds were actually similar for the fingernail as for the fingertip. Seah and colleagues [18] argue that their study "highlights the role of the nail plate as an active agent for sensory perception" (pg. 2163). These results, however, are limited by the use of the two-point discrimination threshold, which has been widely criticised and which is not generally accepted as a valid measure of spatial sensitivity [19]. Moreover, that study investigated only the most basic forms of tactile sensitivity, leaving unclear whether the fingernails support higher-level forms of tactile spatial perception, such as precise localisation of stimuli.

The proposal that the fingernail has active sensory functions is consistent with evidence that there are numerous mechanoreceptors in the nail bed and borders of the nail. Studies in humans have revealed Merkel cells within the nailbed [20,21] while Ruffini endings appear even more common at the base of nails than in the skin itself [22]. Microneurographic recordings from the median nerve of humans have revealed slowly-adapting mechanoreceptors along the borders of the fingernails which respond both to pressure applied to the fingernails [23] and fingertips [24], as well as movements of the distal finger segment [25]. The fingernails thus appear equipped with a rich array of sensory receptors which could potentially support many forms of tactile perception.

The present study investigated a fundamental perceptual ability on the fingernails, namely whether humans can precisely localise tactile stimuli applied to them. Neurological studies have shown that the ability to localise tactile stimuli on the body can be selectively impaired following brain damage [26,27], leaving intact more basic features of touch such as detection and two-point discrimination. Neurocognitive models of higher-level somatoperception have emphasised that tactile localisation is a process distinct from and subsequent to basic processing of touch [28,29]. It is therefore important to understand whether the fingernails support higher-level aspects of touch like localisation, as well as the more basic processes described before [18]. I therefore applied touch to 9 locations on the nail of the left middle finger and measured localisation performance using an established paradigm which has been widely used on other parts of the hand [30]. The results showed that participants are able to localise touch on the fingernail with a high degree of precision.

Method

Participants

Nineteen members of the Birkbeck community (13 women, 6 men) between 20 and 54 years of age (*M*: 34.9, *SD*: 10.1) participated in Experiment 1 for payment or course credit. All participants were right-handed as assessed by the Edinburgh Inventory [31] (*M*: 80.5, *SD*: 22.5). Data from one additional participant was excluded from analyses because the photograph of stimulus locations on the fingertip was missing. Participants gave written informed consent and procedures were approved by

the School of Psychological Sciences Research Ethics Committee at Birkbeck (approval number 2223017).

An additional 19 people (13 women, 6 men) between 18 and 60 years of age (M: 30.2, SD: 12.4) participated in Experiment 2. All but two participants were right handed (M: 66.2, SD: 51.4). One additional participant was tested, but was excluded from the main analyses because they had acrylic nails.

Regarding sample size, the key question in this experiment concerns whether people are able to spatial localise stimulation applied to fingernails at all. This is a quite different question than that in other studies using this paradigm [30], which took for granted that participants would localise touch on the skin at above chance levels. This question is more similar to the study of Miller and colleagues [32] who investigated the ability of people to localise touch applied to a held rod. Miller and colleagues quantified the ability of participants to localise on the rod by using linear regression to quantify how judged location along the rod varied as a function of the actual location of touch. With chance performance, the slope of this regression line should on average equal 0, whereas with perfect performance it should on average equal 1. The ability to localise can thus be tested using a one-sample t-test comparing the mean regression slope across participants to 0, as in the study of Miller and colleagues.

This analysis was not conducted on previous studies using this paradigm to localise touch on the hands, again because the ability of participants to localise above chance was taken for granted. We therefore analysed the raw data from the study of Margolis and Longo [33], regressing judged stimulus location on actual location, separately for the x- and y-coordinates in Bookstein space [34]. Bookstein coordinates work by defining two specific landmarks as points (0,0) and (1,0) of a coordinate system, with all other points scaled accordingly. Of the relevant conditions, the smallest effect size was $d = 3.751$. I aimed to have power to detect localisation performance on the fingernail of one quarter than found for the skin. I therefore divided this effect size by four (i.e., $d = 0.938$). A power analysis using G*Power 3.1 for a one-sample t-test (2-tailed) with alpha of .05 and power of .90 indicated that 15 participants were necessary. To provide a buffer in case of problems with individual participants, I recruited 20 participants in each experiment, of which 19 ended up providing usable data.

Procedures

Experiment 1. At the start of the study, participant-specific visual stimuli were created by taking photographs of the fingernail and fingertip which were then edited using GIMP 2.10.32 software. Each photograph was cropped to include the entire fingernail or the entire distal phalanx of the finger, resulting in 750x750 pixel images (as shown in Figure 1) which were then used for the main experiment.

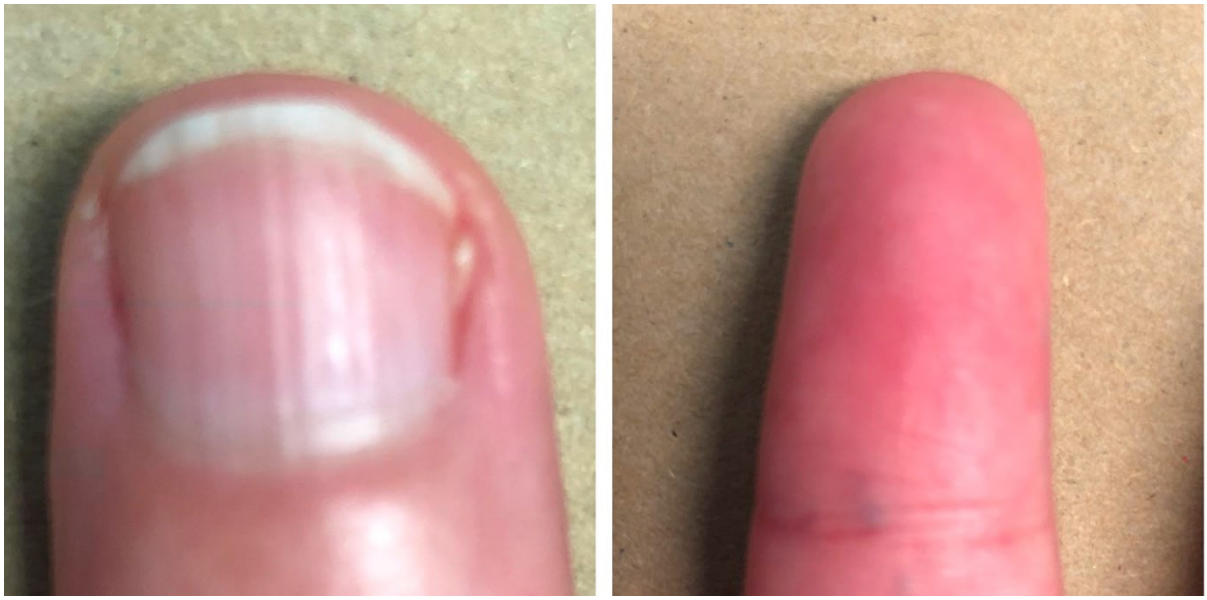

Figure 1: An example of a participant-specific images of the fingernail (left panel) or fingertip (right panel) used to collect responses.

The stimulus was a wooden cuticle pusher stick (Superdrug, London, UK) which tapered to a point of approximately 1 mm in diameter. Stimuli were applied manually by the experimenter for approximately 1 second. Following the procedure used by Seah and colleagues [18], the stick was applied until blanching was apparent on the nailbed or skin, which allowed at least partial standardisation of pressure.

Before the start of the experiment, a square 3x3 grid was drawn on both the fingernail and fingertip of the middle finger of the participant's left hand using a black pen. The size of the grid was varied to take up the entire width of the fingernail or fingertip. A photograph was taken of the marks on each surface with a ruler in the image to allow conversion of distances between pixels and cm. On average, the spacing between adjacent locations was 3.44 mm (*SD*: 0.39) on the fingernail and 4.55 mm (*SD*: 0.79) on the fingertip.

The participant's task was to judge the perceived location of each tactile stimulus by positioning the mouse cursor (a thin crosshair) on the corresponding location of a photograph of their fingernail or fingertip shown on the monitor. The mouse cursor was placed at a different random location on the monitor at the start of each trial to prevent reliance on the location of previous responses. The experiment was controlled by a custom MATLAB (Mathworks, Natick, MA) script.

There were 4 blocks of trials, 2 each of the fingernail and fingertip conditions. The order of blocks was counterbalanced across participants using an ABBA design. Each block consisted of 3 repetitions of each of the 9 locations in random order. This resulted in 27 trials per block and 108 trials overall.

Raw data and the script used to run the study are available here: https://osf.io/63u9j/

Experiment 2. The procedures for the second experiment were similar to Experiment 1 with three changes. First, the stimulus was a von Frey hair producing 15 g of pressure (North Coast Medical, Morgan Hill, CA) instead of a stick. This allowed the pressure applied to the fingernail to be precisely controlled, across trials, surfaces, and participants. The 15 g von Frey hair was chosen because it produced a clearly detectable

sensation and was less prone to slip when applied to the fingernail than larger forces. Second, the stimulated finger was the thumb, rather than the middle finger. The use of a different finger allowed localisation ability to be generalised beyond the specific finger used in Experiment 1. On average, the spacing between adjacent locations was 5.83 mm (*SD*: 1.14) on the fingernail and 4.50 mm (*SD*: 0.90) on the fingertip.

Finally, one concern about Experiment 1 is that the stimulated finger was resting on the tabletop. This means that stimulation applied to the fingernail results in the fingertip being pressed against the table (and vice versa). This raises the possibility that localisation of touch on the fingernail could be driven by pressure on the fingertip. To exclude this possibility, in Experiment 2 the stimulated thumb was held above the table. For the fingernail condition, the little finger rested on the table with the thumb held parallel to the tabletop. For the fingertip condition, the four fingers were made into a fist, with the thumb rolled underneath and the forearm placed in extreme pronation with the wrist resting on the table. These postures are shown in Figure 2.

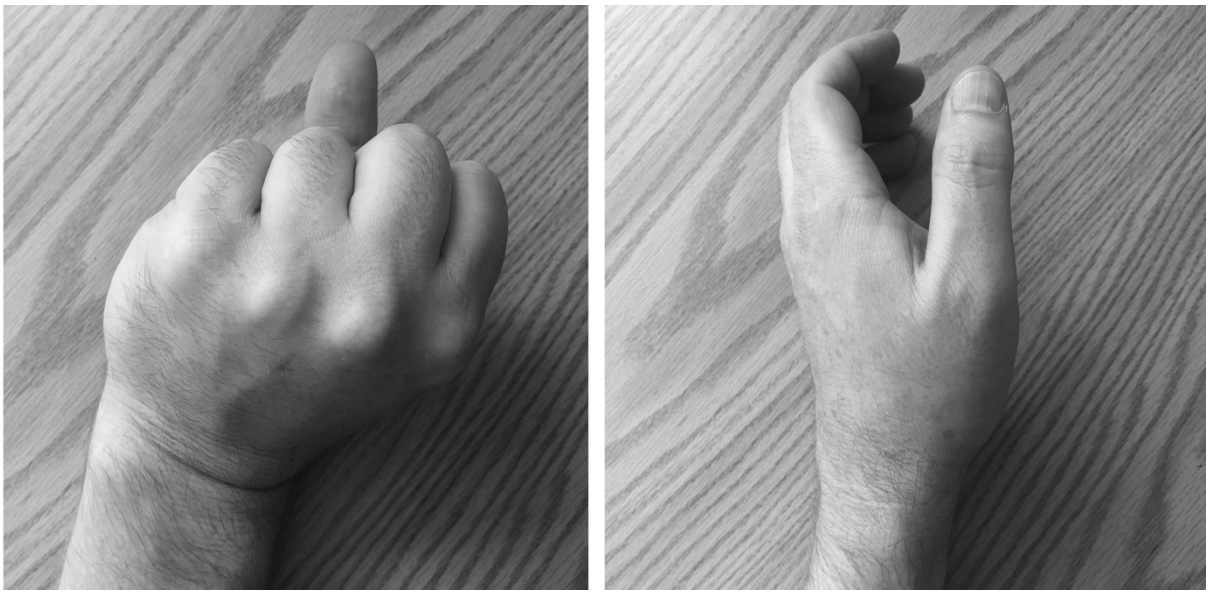

Figure 2: The hand postures used in Experiment 2 for stimulation of the fingertip (left panel) and the fingernail (right panel).

Analysis

The first analysis used Procrustes alignment [35] to superimpose the overall spatial configuration of localisation judgments with the spatial configuration of actual stimulus locations. Procrustes alignment translates, scales, and rotates spatial configurations to align them as closely as possible, without distorting the relative spatial locations of points.

Procrustes alignment was used in two ways. First, it was used to visualise the pattern of localisation responses as a perceptual map, as shown in Figure 2 below. Second, the Procrustes distance (i.e., the residual shape difference remaining between configurations after being placed into Procrustes alignment) was used to quantify the dissimilarity between each participant's perceptual map and a perfectly square map. A null distribution was created using 1 million simulations of random data in a custom MATLAB script. This allows the statistical significance of each participant's localisation performance to be calculated. A null distribution for the grand average Procrustes distance was created by taking 1 million samples of 19 values from the previously

described distribution of simulations, allowing the statistical significance at the population level to be calculated.

The use of a perfectly square grid for these analyses is an approximation. As both the fingertip and fingernail are curved surfaces, the photographs of the fingers used for both coding of stimulus locations and participants' responses will be slightly distorted. For this reason, Procrustes analyses were also run using the coded values of stimulus locations from photographs of each participant's hand. This required that separate simulations of the null distribution (10,000 samples each) be generated for each surface of each participant. These analyses reached identical conclusions in terms of statistical significance as the analyses using a square grid. For this reason, only the latter results are reported, since they are much clearly to depict graphically since they have a common null distribution.

The second analysis was based on the regression approach used by Miller and colleagues [32] to assess tactile localisation performance on a held tool, as mentioned in the power analysis above. In this method, judged location is regressed on actual location for each participant separately. If participants have no ability to localise, then on average the slope of regression lines should equal 0. In contrast, if participants have perfect performance, then regression slopes should equal 1. The ability of participants to localise at better than chance levels can thus be assessed using a one-sample t-test comparing the mean regression slope to 0.

In the study of Miller and colleagues [32], location was judged along the one-dimensional length of the tool. In the present study, in contrast, localisation is made in two-dimensional space. Separate regression analyses were therefore conducted in the proximal-distal finger axis (i.e., *along* finger length) and in the medio-lateral axis (i.e., *across* finger width). These axes were operationalised using the two-point registration method developed by Bookstein [34] 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. For the fingertip, these landmarks were the centre of the crease at the distal interphalangeal joint (i.e., at the base of the distalmost finger segment) and the tip of the finger (i.e., the distalmost point at the centre of the finger). For the fingernail, these landmarks were the base of the fingernail (i.e., where the cuticle ends in the centre of the nail) and the tip of the fingernail (i.e., the distal-most point at the centre of the nail). These landmarks were coded both for the photographs showing the actual locations of the marks made on the fingers and for responses on the monitor, resulting in both stimuli and responses being represented in a common coordinate system. Four linear regression analyses were conducted for each participant, one in each orientation on both the fingertip and fingernail. Mean regression coefficients were compared to 0 using one-sample t-tests. Analysis of variance (ANOVA) was used to assess effects of orientation and body part. ANOVAs were conducted using JASP v. 0.16.1.

In Experiment 2, a few participants noted that the extreme pronated posture adopted for the fingertip stimulation produced left-right confusion when mapping the felt location of touch onto the image of the fingertip. Indeed, 5 participants had large negative regression slopes specifically for the medio-lateral axis of the fingertip condition, suggesting that they had inverted left and right. No negative regression slopes were obtained from any participant in the proximo-distal axis of the fingertip or in either axis of the fingernail. For Figure 6 and for comparison of regression slopes between axes and surfaces, I therefore used the absolute values of these regression coefficients. This, however, would not be valid for the one-sample t-test comparing mean regression slope to 0, so for that test specifically the negative values were

retained. For this reason, analyses using Procrustes distance were altered to allow the possibility of a reflection component, which resulted in the simulated null distributions being different between the two experiments.

Finally, we also calculated the variability of responses across trials in which the same skin location had been stimulated. For each stimulus location, the standard deviation of the Bookstein x- and y-coordinates was calculated and averaged across the 9 stimulus locations within each skin surface. ANOVA was again used to assess effects of orientation and body part.

Results

Experiment 1

The top panel of Figure 3 shows perceptual maps of tactile localisation judgments on the fingertip (left panel) and fingernail (right panel) with Procrustes alignment used to superimpose maps across participants. It is clear from the figure that the 9 stimulus locations are placed into the correct relative positions, showing that tactile stimuli on the fingertips can be localised effectively. This effect was quantified by calculating the Procrustes distance between each participant's perceptual map and a square grid and comparing these to null distributions calculated by simulation, as shown in the bottom panel of Figure 3, which allowed us to calculate a p-value for each participant's map. Significant localisation, indexed by a Procrustes distance smaller than expected by chance, was found for all 19 participants on the fingertip (all p's < .0001; bottom left panel) and on the fingernail (all p's < .01; bottom centre panel). Grand mean Procrustes distances were compared to a null distribution in which simulated data from 19 participants was generated. Data for both the fingertip (M: .091, SD: .045) and fingernail (M: .126, SD: .100) was far lower than any values obtained in simulations (bottom right panel). While Procrustes distances were on average modestly higher on the fingernail than on the fingertip, this difference did not reach statistical significance, $t(18) = 1.87$, $p = .078$, $d_z = 0.429$.

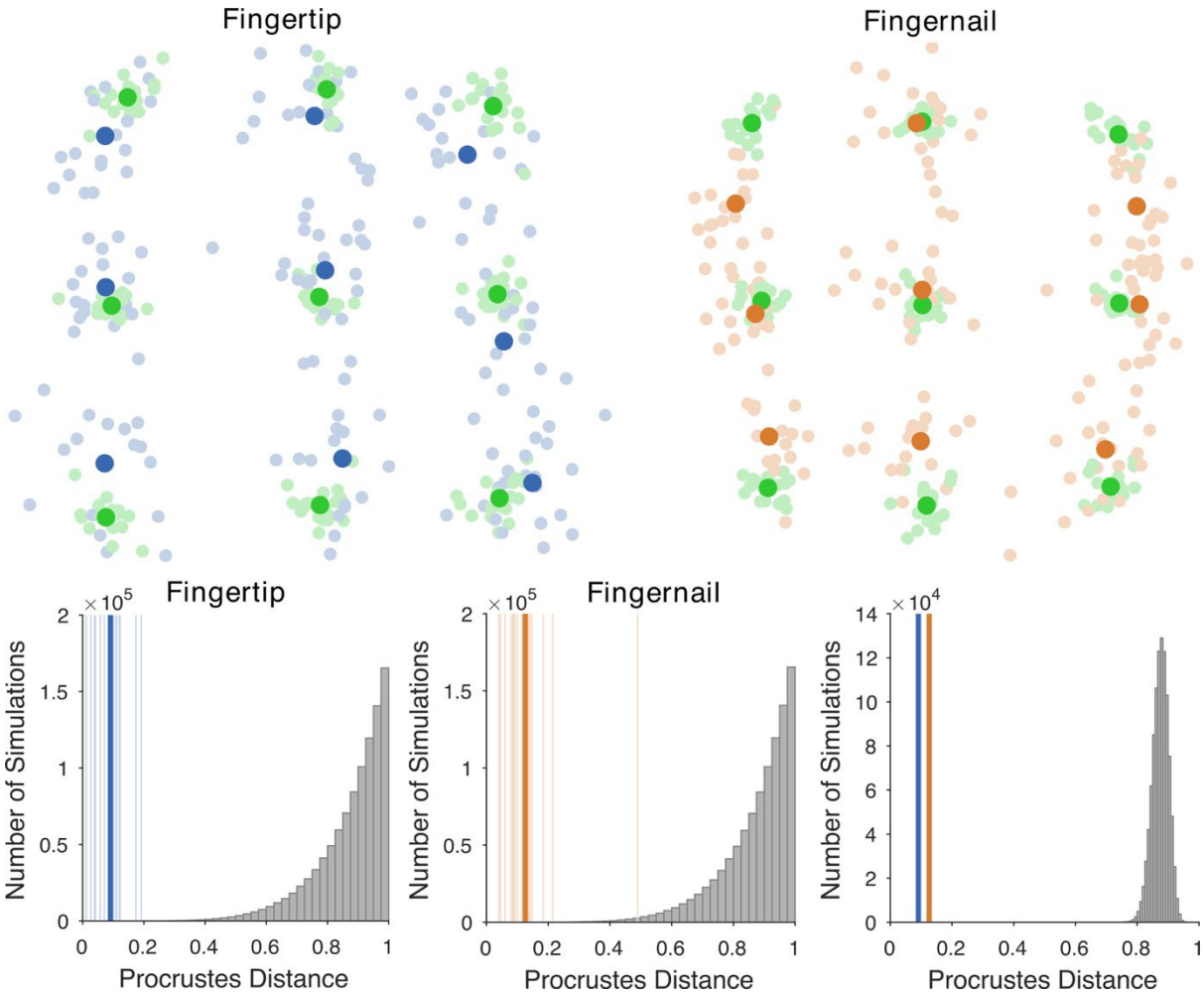

Figure 3: Results from Experiment 1. *Top row*: Maps of the nine actual stimulus locations (in green) and judged locations on the fingertip (in blue; top left) and fingernail (in orange; top right) placed into Procrustes alignment. Dark marks indicate grand means across participants while lighter marks show mean values for each individual participant. *Bottom row*: Procrustes distances comparing perceptual maps to square grids on the fingertip (bottom left) and fingernail (bottom centre). Thin vertical lines are individual participants, while thick lines are grand means. The grey histograms show a null distribution generated from simulations of single participants (bottom left and centre) and from simulations of a sample of 19 participants (bottom right).

The results from the regression analysis are shown in the left panel of Figure 4. On the skin of the fingertip, performance was unsurprisingly high. Mean regression slopes were high and substantially greater than 0 both along finger length (M: 0.975, SD: 0.258), $t(18) = 16.47$, $p < .0001$, $d = 3.780$, and across finger width (M: 1.196, SD: 0.193), $t(18) = 27.02$, $p < .0001$, $d = 6.199$.

More importantly, performance was also significantly above chance levels on the fingernail. Regression slopes were significantly higher than 0 both along fingernail length (M: 0.660, SD: 0.228), $t(18) = 12.61$, $p < .0001$, $d = 2.893$, and across fingernail width (M: 0.966, SD: 0.235), $t(18) = 17.92$, $p < .0001$, $d = 4.110$. These results show clearly that participants are able to localise touches applied to the fingernail. Indeed, regression slopes were greater than 0 for all 19 participants in both orientations.

A repeated measures ANOVA revealed a significant main effect of body part, $F(1, 18) = 50.67$, $p < .001$, $\eta^2 = .305$, with lower slopes on the fingernail than the fingertip. There was also a main effect of orientation, $F(1, 18) = 33.50$, $p < .0001$, $\eta^2 = .285$, with lower slopes along finger length than across finger width. There was no significant interaction between the two factors, $F(1, 18) = 0.95$, $p = .343$, $\eta^2 = .007$. Clear effects of orientation were found both on the fingertip, $t(18) = 3.12$, $p < .01$, $d_z = 0.716$, and on the fingernail, $t(18) = 5.64$, $p < .0001$, $d_z = 1.294$.

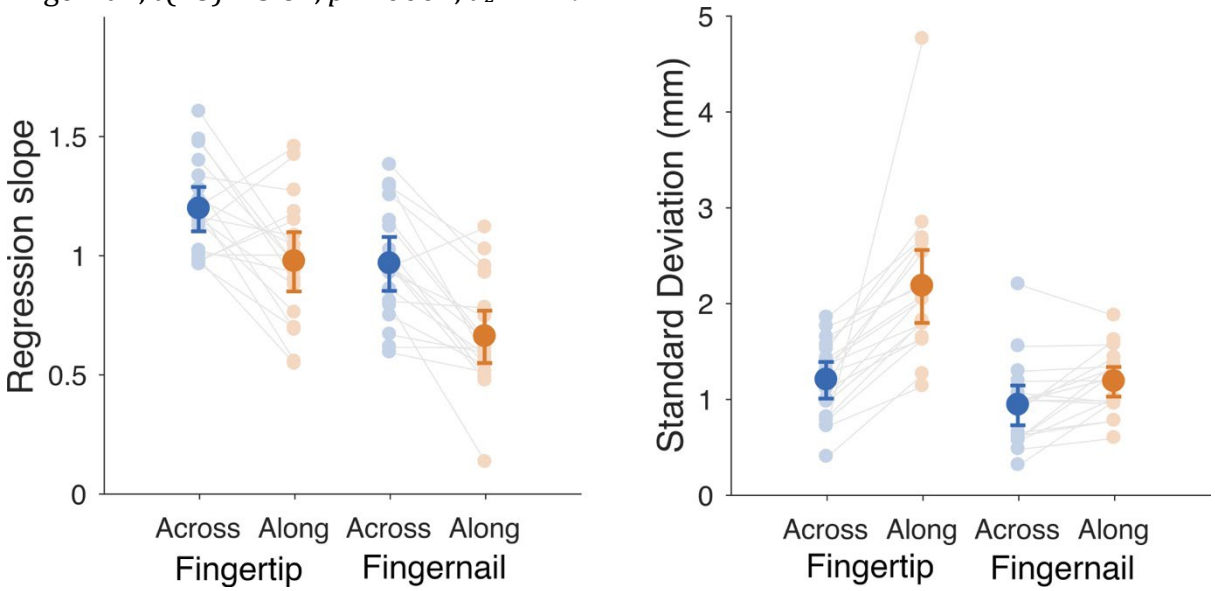

Figure 4: Results from Experiment 1. *Left panel*: mean slopes regressing judged stimulus location on actual location in both orientations on the fingertip and fingernail. If participants were unable to localise touch, slopes should on average be 0. *Right panel*: mean standard deviation of responses in each orientation averaged across the 9 stimulus locations. Error bars are 95% confidence intervals.

The right panel of Figure 4 shows the standard deviation of responses in both orientations. An ANOVA showed a significant main effect of orientation, $F(1, 18) = 33.09$, $p < .0001$, $\eta^2 = .273$, with higher precision across finger width than along finger length. This pattern was present for both the fingertip, $t(18) = 5.27$, $p < .0001$, $d_z = 1.210$, and the fingernail, $t(18) = 3.39$, $p < .005$, $d_z = 0.777$, and is consistent with the results of previous studies that measured precision of tactile localisation on the hand dorsum [33,36]. There was also a significant main effect of body part, $F(1, 18) = 64.83$, $p < .0001$, $\eta^2 = .288$, which was modulated by a significant interaction between body part and orientation, $F(1, 18) = 15.72$, $p < .001$, $\eta^2 = .098$. This interaction showed that the effect of orientation was larger on the fingertip than on the fingernail.

Experiment 2

The top panel of Figure 5 shows perceptual maps of tactile localisation judgments on the fingertip (left panel) and fingernail (right panel). As in Experiment 1, the ability of participants to localise touch on both the fingertip and fingernail is immediately apparent from the maps.

The bottom panel of Figure 5 shows Procrustes distances between each participant's perceptual map and a square grid. As in Experiment 1, significant localisation, indexed by a Procrustes distance smaller than expected by chance, was found for all participants on the fingernail (all p's < .05; bottom centre panel), and for 18

of 19 participants on the fingertip (bottom left panel). The bottom right panel of Figure 5 shows grand mean Procrustes distances, which were substantially smaller than any values obtained in simulations on both the fingertip (*M*: .212, *SD*: .148) and fingernail (*M*: .233, *SD*: .159). As in Experiment 1, Procrustes distances were on average slightly higher for the fingernail than the fingertip, but this did not reach statistical significance, $t(18) = 0.48$, $p = .64$, $d_z = 0.109$.

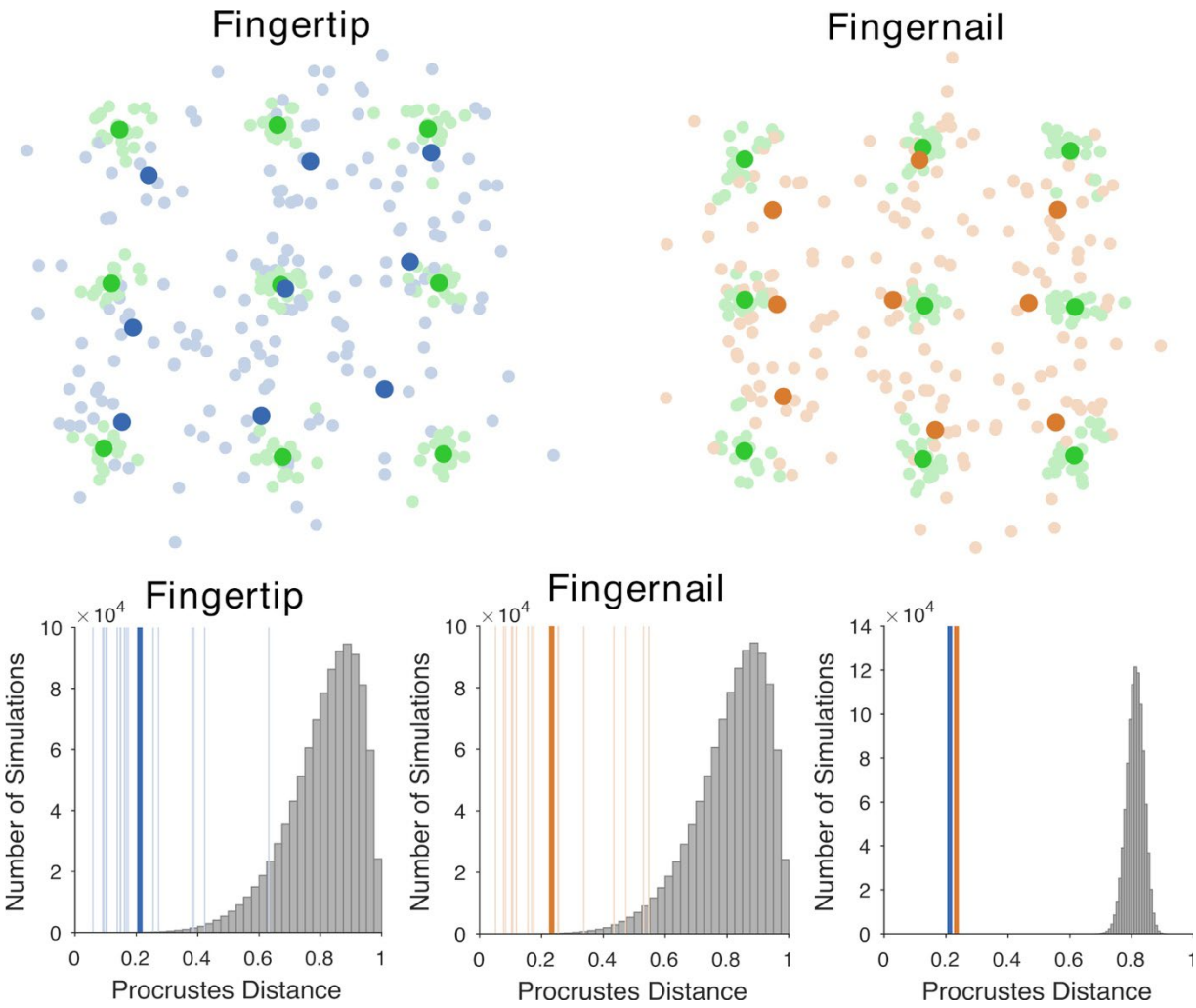

Figure 5: Results from Experiment 2. *Top row*: Maps of the nine actual stimulus locations (in green) and judged locations on the fingertip (in blue; top left) and fingernail (in orange; top right) placed into Procrustes alignment. Dark marks indicate grand means across participants while lighter marks show mean values for each individual participant. *Bottom row*: Procrustes distances comparing perceptual maps to square grids on the fingertip (bottom left) and fingernail (bottom centre). Thin vertical lines are individual participants, while thick lines are grand means. The grey histograms show a null distribution generated from simulations of single participants (bottom left and centre) and from simulations of a sample of 19 participants (bottom right).

The results from the regression analysis are shown in the left panel of Figure 6. On the fingertip, regression slopes were significantly higher than 0, both along finger length (*M*: 0.837, *SD*: 0.315), $t(18) = 11.60$, $p < .0001$, $d = 2.661$, and across finger width

(*M*: 0.554, *SD*: 0.824), $t(18) = 2.93$, $p < .01$, $d = 0.673$. Performance was also well above chance levels on the fingernail, with regression slopes greater than 0 both along fingernail length (*M*: 0.680, *SD*: 0.235), $t(18) = 12.61$, $p < .0001$, $d = 2.893$, and across fingernail width (*M*: 0.756, *SD*: 0.304), $t(18) = 10.84$, $p < .0001$, $d = 2.486$. As in Experiment 1, regression slopes on the fingernail were positive for all 19 participants in both orientations.

An ANOVA on regression slopes showed a marginally significant effect of body part, $F(1, 18) = 4.11$, $p = .058$, $\eta^2 = .186$; as in Experiment 1, slopes were slightly higher on the fingertip than the fingernail. There was no significant effect of orientation, $F(1, 18) = 0.75$, $p = .397$, $\eta^2 = .040$, nor an interaction, $F(1, 18) = 0.04$, $p = .838$, $\eta^2 = .002$.

The right panel of Figure 6 shows the standard deviation of responses in both orientation. An ANOVA showed no significant effects of body part, $F(1, 18) = 1.70$, $p = .209$, $\eta^2 = .046$, orientation, $F(1, 18) = 2.21$, $p = .155$, $\eta^2 = .033$, nor an interaction, $F(1, 18) = 0.05$, $p = .827$, $\eta^2 = .004$.

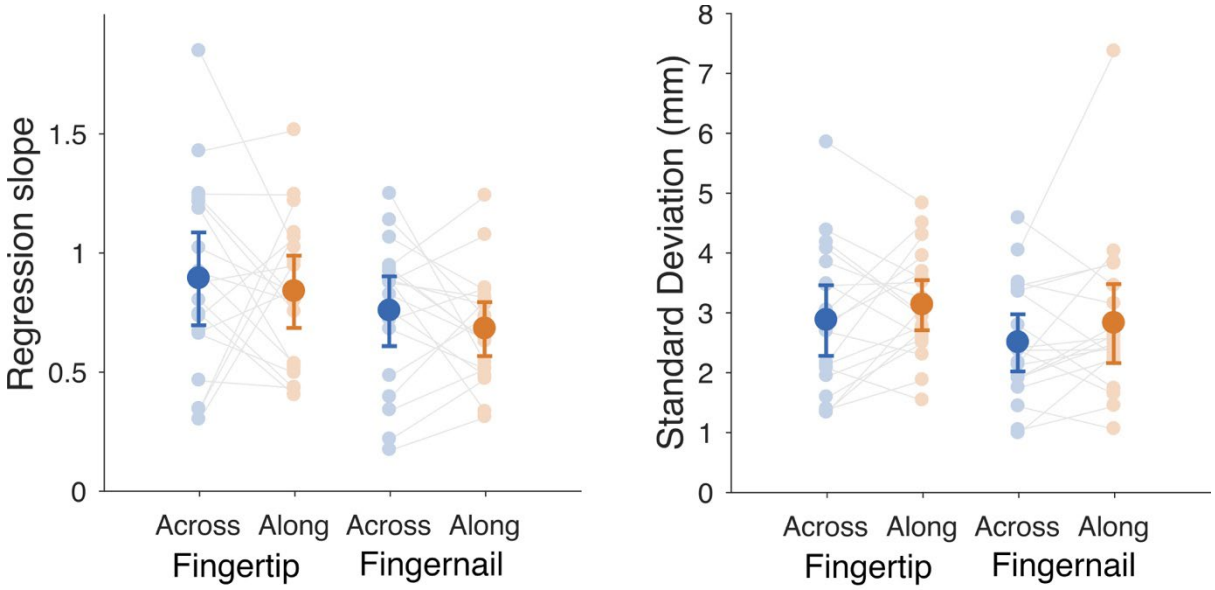

Figure 6: Results from Experiment 2. *Left panel*: mean slopes regressing judged stimulus location on actual location in both orientations on the fingertip and fingernail. *Right panel*: mean standard deviation of responses in each orientation averaged across the 9 stimulus locations. Error bars are 95% confidence intervals.

Discussion

This study shows that people can localise tactile stimuli applied to the fingernail. Localisation performance on the fingernail was above chance levels for all participants tested, and broadly comparable to performance on the fingertip itself. These results complement findings showing that participants can detect pressure and discriminate one from two touches on the nail plate [18], but extend this line of research to a more complex spatial judgment.

The ability to localise touch on the fingernails may be related to recent research which has shown that people can localise touch applied to a stick which is held in the hand [32]. In both cases, the precise location of a stimulus is perceived despite the absence of any tactile receptors within the stimulated surface itself. Numerous authors

over the past 400 years have commented on the ability to perceive stimuli at the end of a long cane, such as widely used by blind people [17,37–39]. The contribution of Miller and colleagues [32] was to show that it is not just the people can perceive touch at the distal end of the tool, but that they have precise information about the exact location of stimulation along the tool's length. The present results, analogously, show that it is not just the people can perceive touch applied to the distal extremity of the fingernail, as emphasised by Katz [16] and Gibson [17], but instead that people can tell precisely where on the fingernail a stimulus was applied. Indeed, comparing mean regression slopes, performance in the proximo-distal axis of the fingernail in this study (mean slope: 0.660) is similar to that found for passive touch applied to a long stick (mean slope: 0.57) [32].

Anatomical studies of mechanoreceptors in the nailbed have identified populations of slowly-adapting receptors, including Merkel cells [20,21] and Ruffini corpuscles [22]. The fingernails are known to be sensitive to fingernail forces, as shown for example by the ability of fingernail imaging to recover the forces applied to the pulp of the fingertip [40]. Similarly, reducing the rigidity of the fingernail by moistening reduces perceptual sensitivity to discriminating fingertip forces [15]. Microneurographic studies of the median nerve have identified slowly-adapting mechanoreceptors along the borders of the fingernail [23,24]. These slowly-adapting (SA) responses, particularly SA-I fibers associated with Merkel cells, may underlie the precise spatial localisation ability described in this study. SA-II responses associated with Ruffini endings may also be involved. A recent study showed the intraneural stimulation of SA-II units in the fingernails produced clear experiences of pressure being applied to the nail [41]. Notably, however, Miller and colleagues [32] linked tactile localisation on tools to rapidly-adapting Pacinian corpuscles, which can derive estimates of location from the pattern of vibrations across the hand. While Pacinian corpuscles have not, to my knowledge, been identified in the nailbed itself, these cells lie deep with the dermis and can detect vibrations from widespread regions of the hand. Thus, populations of Pacinian cells could potentially code information about the precise location of stimuli applied to the fingernail, even if these cells are located in distant regions of the skin, analogous to the way in which they can code information about the location of stimuli on a long tool.

Tactile localisation on the fingernail was more accurate and less variable in the medio-lateral finger axis than in the proximo-distal axis. This is consistent with the pattern found at other locations on the dorsal surface of the hand in localisation tasks [33,36], as well as in other tasks assessing spatial acuity [42,43], tactile distance perception [44,45], and proprioceptive localisation judgments [46]. Surprisingly, similar anisotropy was also found at the fingertip. While anisotropy has been reported on the glabrous skin of the palm for both tactile acuity [47] and tactile distance perception [48], it has been less obvious on the fingertip [47]. One possibility is that apparent anisotropy on the fingertip is an artefact of the fact that the distal phalanx of the finger is itself elongated, such that participants had more space in which to respond in the proximo-distal finger axis than in the medio-lateral axis. This is very different to the fingernails, which are not longer than they are wide and for which the grid of stimulation points took up nearly the entire space of potential responses.

In conclusion, the present results show that the human fingernail is capable of highly precise spatial localisation of touch. While the functional implications of this ability remain uncertain, this finding is consistent with claims that that the fingernails may have important roles in sensorimotor function [16,17]. The full extent of the

sensory capabilities of the fingernails remains unknown. It will be important for future research to further explore the ways in which the fingernails enhance sensory function and how this contributes to manual dexterity. It will also be interesting to determine whether this ability is specific to fingernails, or whether tactile stimuli can also be precisely located on toenails.

References

1. Le Gros Clark WE. 1959 *The antecedents of man*. Edinburgh University Press.

2. Wood Jones F. 1916 *Arboreal man*. Arnold.

3. Spearman RIC. 1985 Phylogeny of the nail. *J Hum Evol* **14**, 57–61. (doi:10.1016/S0047-2484(85)80095-6)

4. Hamrick MW. 2001 Development and evolution of the mammalian limb: Adaptive diversification of nails, hooves, and claws. *Evol Dev* **3**, 355–363. (doi:10.1046/j.1525-142X.2001.01032.x)

5. Bloch JI, Boyer DM. 2002 Grasping primate origins. *Science* **298**, 1606–1610. (doi:10.1126/science.1078249)

6. Le Gros Clark WE. 1936 The problem of the claw in primates. *Proc Zool Soc London* **106**, 1–24. (doi:10.1111/j.1096-3642.1936.tb02276.x)

7. Baran R. 2010 The burden of nail psoriasis: An introduction. *Dermatology* **221**, 1–5. (doi:10.1159/000316169)

8. Lubeck DP, Patrick DL, McNulty P, Fifer SK, Birnbaum J. 1993 Quality of life of persons with onychomycosis. *Qual Life Res* **2**, 341–348. (doi:10.1007/BF00449429)

9. Zook EG, Guy RJ, Russell RC. 1984 A study of nail bed injuries: Causes, treatment, and prognosis. *J Hand Surg* **9**, 247–252. (doi:10.1016/S0363-5023(84)80153-7)

10. Dumontier C. 2003 Distal replantation, nail bed, and nail problems in musicians. *Hand Clinics* **19**, 259–272. (doi:10.1016/S0749-0712(02)00135-X)

11. Prandi G, Caccialanza M. 1977 An unusual congenital nail dystrophy ('soft nail disease'). *Clin Exp Dermatol* **2**, 265–269. (doi:10.1111/j.1365-2230.1977.tb02567.x)

12. Napier JR. 1993 *Hands, Revised Ed.* Princeton University Press.

13. Kleinert HE, Putcha SM, Ashbell TS, Kutz JE. 1967 The deformed finger nail, a frequent result of failure to repair nail bed injuries. *J Trauma* **7**, 177–190. (doi:10.1097/00005373-196703000-00001)

14. Zook EG. 2003 Anatomy and physiology of the perionychium. *Clin. Anat.* **16**, 1–8. (doi:10.1002/ca.10078)

15. Brothers T, Hollins M. 2014 Two sensory channels mediate perception of fingertip force. *Perception* **43**, 1071–1082. (doi:10.1068/p7790)

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

17. Gibson JJ. 1966 *The senses considered as perceptual systems*. Houghton Mifflin.

18. Seah BZQ, Wu CCH, Sebastin SJ, Lahiri A. 2013 Tactile sensibility on the fingernail. *J Hand Surg* **38**, 2159–2163. (doi:10.1016/j.jhsa.2013.08.112)

19. Craig JC, Johnson KO. 2000 The two-point threshold: Not a measure of tactile spatial resolution. *Curr Dir Psychol Sci* **9**, 29–32. (doi:10.1111/1467-8721.00054)

20. Moll I, Moll R. 1993 Merkel cells in ontogenesis of human nails. *Arch Dermatol Res* **285**, 366–371. (doi:10.1007/BF00371838)

21. Cameli N, Ortonne JP, Picardo M, Peluso AM, Tosti A. 1998 Distribution of Merkel cells in adult human nail matrix. *Brit J Dermatol* **139**, 541–541. (doi:10.1046/j.1365-2133.1998.02430.x)

22. Paré M, Behets C, Cornu O. 2003 Paucity of presumptive Ruffini corpuscles in the index finger pad of humans. *J Comp Neurol* **456**, 260–266. (doi:10.1002/cne.10519)

23. Johansson RS. 1978 Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptive units in the glabrous skin area. *J Physiol* **281**, 101–125. (doi:10.1113/jphysiol.1978.sp012411)

24. Birznieks I, Macefield VG, Westling G, Johansson RS. 2009 Slowly adapting mechanoreceptors in the borders of the human fingernail encode fingertip forces. *J Neurosci* **29**, 9370–9379. (doi:10.1523/JNEUROSCI.0143-09.2009)

25. Knibestöl M. 1975 Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *J Physiol* **245**, 63–80. (doi:10.1113/jphysiol.1975.sp010835)

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

27. Halligan PW, Hunt M, Marshall JC, Wade DT. 1995 Sensory detection without localization. *Neurocase* **1**, 259–266. (doi:10.1080/13554799508402370)

28. Medina J, Coslett HB. 2010 From maps to form to space: Touch and the body schema. *Neuropsychologia* **48**, 645–654. (doi:10.1016/j.neuropsychologia.2009.08.017)

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

30. Mancini F, Longo MR, Iannetti GD, Haggard P. 2011 A supramodal representation of the body surface. *Neuropsychologia* **49**, 1194–1201. (doi:10.1016/j.neuropsychologia.2010.12.040)

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

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

33. Margolis AN, Longo MR. 2015 Visual detail about the body modulates tactile localisation biases. *Exp Brain Res* **233**, 351–358. (doi:10.1007/s00221-014-4118-3)

34. Bookstein FL. 1991 *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press.

35. Goodall C. 1991 Procrustes methods in the statistical analysis of shape. *J Roy Stat Soc B* **53**, 285–321. (doi:10.1111/j.2517-6161.1991.tb01825.x)

36. Medina S, Tamè L, Longo MR. 2018 Tactile localization biases are modulated by gaze direction. *Exp Brain Res* **236**, 31–42. (doi:10.1007/s00221-017-5105-2)

37. Descartes R. 1637 *La dioptrique [Optics]*.

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

39. James W. 1890 *The principles of psychology*. Dover.

40. Fallahinia N, Mascaro SA. 2020 Comparison of constrained and unconstrained human grasp forces using fingernail imaging and visual servoing. In *2020 IEEE International Conference on Robotics and Automation (ICRA)*, pp. 2668–2674. Paris, France: IEEE. (doi:10.1109/ICRA40945.2020.9196963)

41. Watkins RH, Durao De Carvalho Amante M, Backlund Wasling H, Wessberg J, Ackerley R. 2022 Slowly-adapting type II afferents contribute to conscious touch sensation in humans: Evidence from single unit intraneural microstimulation. *The Journal of Physiology* **600**, 2939–2952. (doi:10.1113/JP282873)

42. Schlereth T, Magerl W, Treede R-D. 2001 Spatial discrimination thresholds for pain and touch in human hairy skin. *Pain* **92**, 187–194. (doi:10.1016/S0304-3959(00)00484-X)

43. Cody FWJ, Garside RAD, Lloyd D, Poliakoff E. 2008 Tactile spatial acuity varies with site and axis in the human upper limb. *Neurosci Lett* **433**, 103–108. (doi:10.1016/j.neulet.2007.12.054)

44. Longo MR, Haggard P. 2011 Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *J Exp Psychol: Hum Percept & Perform* **37**, 720–726. (doi:10.1037/a0021921)

45. Fiori F, Longo MR. 2018 Tactile distance illusions reflect a coherent stretch of tactile space. *Proc Natl Acad Sci* **115**, 1238–1243. (doi:10.1073/pnas.1715123115)

46. Longo MR, Haggard P. 2010 An implicit body representation underlying human position sense. *Proc Natl Acad Sci* **107**, 11727–11732. (doi:10.1073/pnas.1003483107)

47. Gibson GO, Craig JC. 2005 Tactile spatial sensitivity and anisotropy. *Percept & Psychophys* **67**, 1061–1079. (doi:10.3758/BF03193632)

48. Longo MR. 2020 Tactile distance anisotropy on the palm: A meta-analysis. *Atten Percept & Psychophys* **82**, 2137–2146. (doi:10.3758/s13414-019-01951-w)