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Precise tactile localization on the human fingernail

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Fingernails are specialized features of the primate hand, which are believed to contribute to manual dexterity. The sensorimotor functions of fingernails, however, remain poorly understood. This study investigates the ability of humans to precisely localize 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 with stimuli applied to the skin of the fingertip. The results showed that participants are able to localize touch on the fingernails at substantially higher than chance levels. Moreover, the precision of this ability is not appreciably lower than that of the fingertips. These results show that the fingernail is a highly sensitive sensory organ, which is capable of providing rich spatial information about tactile stimuli.

1. Introduction

While most mammals have claws on each digit, a characteristic feature of primates is the presence of nails [1,2] instead of claws. Nails are 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 emphasized, is that the fingernail provides a hard supporting background that 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 the perceptual ability to discriminate forces applied to the fingertip [15]. In this view, the fingernails

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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 recognized even when the objects were touched only with the fingernails. Similarly, James Gibson [17] emphasized 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. (p. 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 *et al.* [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 *et al.* [18] argue that their study 'highlights the role of the nail plate as an active agent for sensory perception' (p. 2163). These results, however, are limited by the use of the two-point discrimination threshold, which has been widely criticized and 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 localization 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 nail bed [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 (SA) 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 of the fingernails, namely whether humans can precisely localize tactile stimuli applied to them. Neurological studies have shown that the ability to localize 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 emphasized that tactile localization 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 localization, as well as the more basic processes described before [18]. I therefore applied touch to nine locations on the nail of the left middle finger or thumb and measured localization 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 localize touch on the fingernail with a high degree of precision.

2. Material and methods

(a) Participants

Nineteen members of the Birkbeck community (13 women and 6 men) between 20 and 54 years of age (*M*: 34.9, s.d.: 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, s.d.: 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 and 6 men) between 18 and 60 years of age (*M*: 30.2, s.d.: 12.4) participated in experiment 2. All but two participants were right-handed (*M*: 66.2, s.d.: 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 spatially localize 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 localize touch on the skin at above chance levels. This question is more similar to the study of Miller *et al.* [32], who investigated the ability of people to localize touch applied to a held rod. Miller *et al.* quantified the ability of participants to localize 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 localize can thus be tested using a one-sample *t*-test comparing the mean regression slope across participants to 0.

This analysis was not conducted on previous studies using this paradigm to localize touch on the hands, again because the ability of participants to localize above chance was taken for granted. I therefore analysed the raw data from the study of Margolis & Longo [33], regressing judged stimulus location on the 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 localization 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 (two-tailed) with an α-value of 0.05 and a power of 0.90 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 whom 19 ended up providing usable data.

(b) Procedures

(i) 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 750 × 750 pixel images (as shown in figure 1), which were then used for the main experiment.

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 *et al.* [18], the stick was applied until blanching was apparent on the nail bed or skin, which allowed at least partial standardization of pressure.

Before the start of the experiment, a square 3 × 3 grid was drawn on both 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 (s.d.: 0.39) on the fingernail and 4.55 mm (s.d.: 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 four blocks of trials, two each of the fingernail and fingertip conditions. The order of blocks was counterbalanced across participants using an ABBA design. Each block consisted of three repetitions of each of the nine locations in random order. This resulted in 27 trials per block and 108 trials overall.

(ii) 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 localization ability to be generalized beyond the specific finger used in experiment 1. On average, the spacing between adjacent locations was 5.83 mm (s.d.: 1.14) on the fingernail and 4.50 mm (s.d.: 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 localization 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.

(c) Analysis

The first analysis used Procrustes alignment [35] to superimpose the overall spatial configuration of localization judgements 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 visualize the pattern of localization responses as a perceptual map, as shown in figures 3 and 5 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

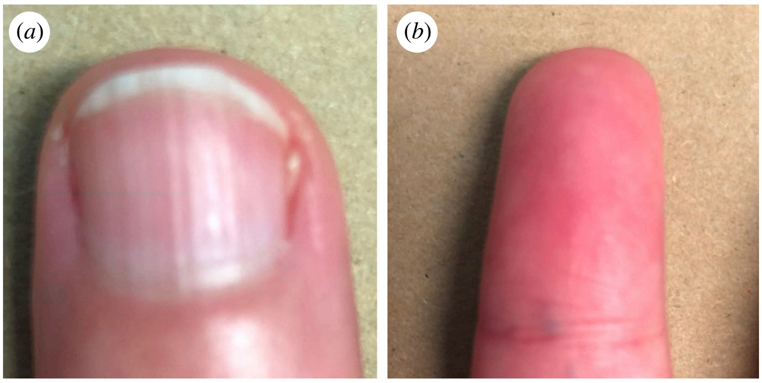

Figure 1. An example of a participant-specific image of the fingernail (*a*) and fingertip (*b*) used to collect responses.

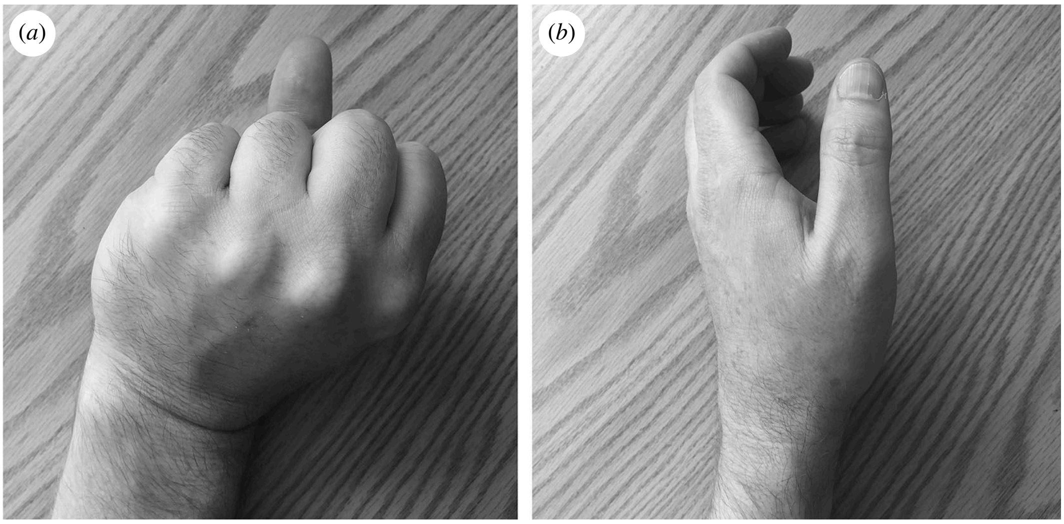

Figure 2. The hand postures used in experiment 2 for stimulation of the fingertip (*a*) and the fingernail (*b*).

data in a custom MATLAB script. This allows the statistical significance of each participant's localization 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, as they are much clearer to depict graphically since they have a common null distribution for both surfaces and all participants.

The second analysis was based on the regression approach used by Miller *et al.* [32] to assess tactile localization performance on a held tool, as mentioned in the power analysis above. In this method, judged location is regressed on the actual location for each participant separately. If participants have no ability to localize, 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 localize 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 *et al.* [32], location was judged along the one-dimensional length of the tool. In the present study, in contrast, localization is made in a two-dimensional space. Separate regression analyses were therefore conducted in the proximal–distal finger axis (i.e. along finger length) and the medio-lateral axis (i.e. across finger width). These axes were operationalized 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 distal-most finger segment) and the tip of the finger (i.e. the distal-most 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 fingertip and fingernail. Mean regression coefficients were compared with 0 using one-sample *t*-tests. Analysis of variance (ANOVA) was used to assess the 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, five 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 the 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 the 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, I 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 nine stimulus locations within each skin surface. ANOVA was again used to assess the effects of orientation and body part.

3. Results

(a) Experiment 1

The top panel of figure 3 shows perceptual maps of tactile localization 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 nine stimulus locations are placed into the correct relative positions, showing that tactile stimuli on the fingertips can be localized 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 localization, indexed by a Procrustes distance smaller than expected by chance, was found for all 19 participants on the fingertip (all p-values < 0.0001; bottom left panel) and on the fingernail (all p-values < 0.01; bottom centre panel). Grand mean Procrustes distances were compared with a null distribution in which simulated data from 19 participants were generated. Data for both fingertip (M: 0.091, s.d.: 0.045) and fingernail (M: 0.126, s.d.: 0.100) 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, $t(18) = 1.87$, $p = 0.078$, $d_z = 0.429$.

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, s.d.: 0.258), $t(18) = 16.47$, $p < 0.0001$, $d = 3.780$, and across finger width (M: 1.196, s.d.: 0.193), $t(18) = 27.02$, $p < 0.0001$, $d = 6.199$.

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, s.d.: 0.228), $t(18) = 12.61$, $p < 0.0001$, $d = 2.893$, and across fingernail width (M: 0.966, s.d.: 0.235), $t(18) = 17.92$, $p < 0.0001$, $d = 4.110$. These results clearly show that participants are able to localize 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 the body part, $F_{1, 18} = 50.67$, $p < 0.001$, $\eta^2 = 0.305$, with lower slopes on the fingernail than the fingertip. There was also a main effect of orientation, $F_{1, 18} = 33.50$, $p < 0.0001$, $\eta^2 = 0.285$, with lower slopes along finger length than across finger width. There was no significant interaction between the two factors, $F_{1, 18} = 0.95$, $p = 0.343$, $\eta^2 = 0.007$. Clear effects of orientation were found both on the fingertip, $t(18) = 3.12$, $p < 0.01$, $d_z = 0.716$, and on the fingernail, $t(18) = 5.64$, $p < 0.0001$, $d_z = 1.294$.

The right panel of figure 4 shows the standard deviation of responses in both orientations. An ANOVA showed a significant main effect of orientation, $F_{1, 18} = 33.09$, $p < 0.0001$, $\eta^2 = 0.273$, with higher precision across finger width than along finger length. This pattern was present for both the fingertip, $t(18) = 5.27$, $p < 0.0001$, $d_z = 1.210$, and the fingernail, $t(18) = 3.39$, $p < 0.005$, $d_z = 0.777$, and is consistent with the results of previous studies that measured precision of tactile localization on the hand dorsum [33,36]. There was also a significant main effect of body part, $F_{1, 18} = 64.83$, $p < 0.0001$, $\eta^2 = 0.288$, which was modulated by a significant interaction between body part and orientation, $F_{1, 18} = 15.72$, $p < 0.001$, $\eta^2 = 0.098$. This interaction showed that the effect of orientation was larger on the fingertip than on the fingernail.

(b) Experiment 2

The top panel of figure 5 shows perceptual maps of tactile localization judgements on the fingertip (left panel) and fingernail (right panel). As in experiment 1, the ability of participants to localize 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 localization, indexed by a Procrustes distance smaller than expected by chance, was found for all participants on the fingernail (all p-values < 0.05; 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 fingertip (M: 0.212, s.d.: 0.148) and fingernail (M: 0.233, s.d.: 0.159). As in experiment 1, Procrustes distances were on average slightly higher for the fingernail than the fingertip, but this did not reach statistical significance, $t(18) = 0.48$, $p = 0.64$, $d_z = 0.109$.

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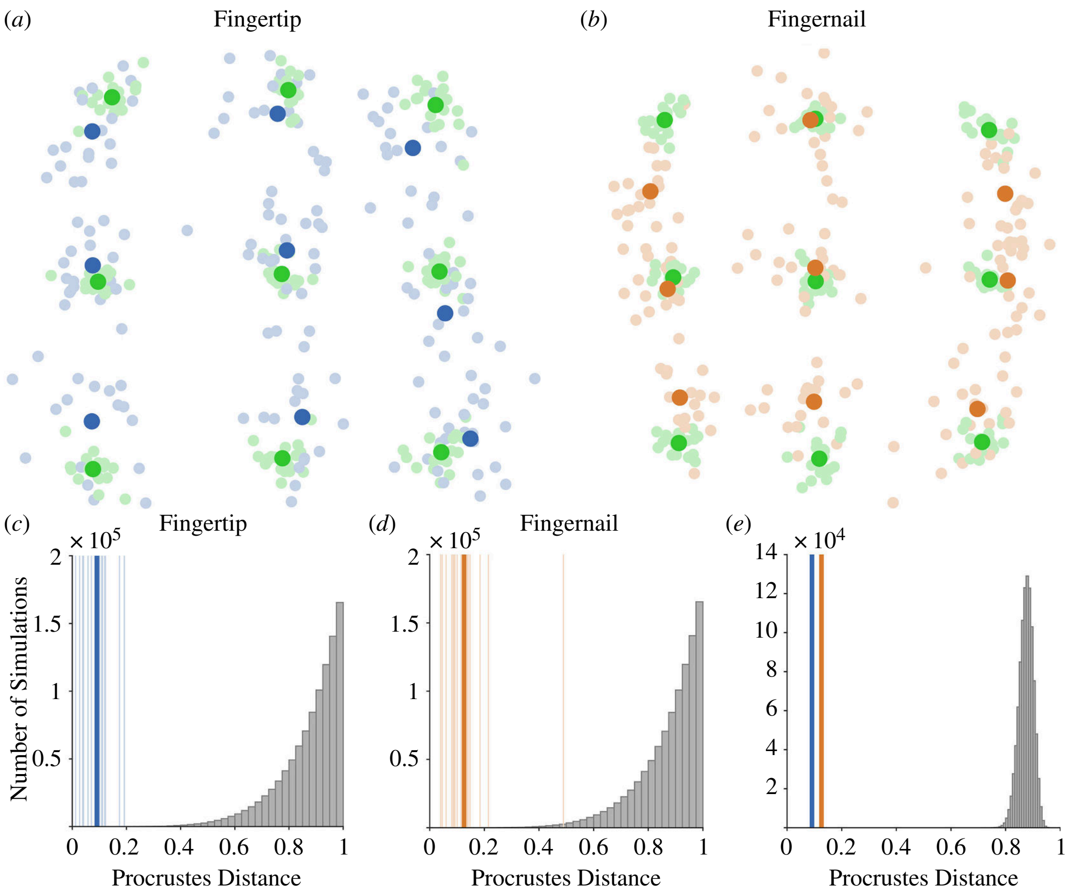

Figure 3. Results from experiment 1. (*a,b*) Maps of the nine actual stimulus locations (in green) and judged locations on the fingertip (in blue; *a*) and fingernail (in orange; *b*) placed into Procrustes alignment. Dark marks indicate grand means across participants, while lighter marks show mean values for each individual participant. (*c–e*) Procrustes distances comparing perceptual maps to square grids on the fingertip (*c*) and fingernail (*d*). 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 (*c,d*) and from simulations of a sample of 19 participants (*e*).

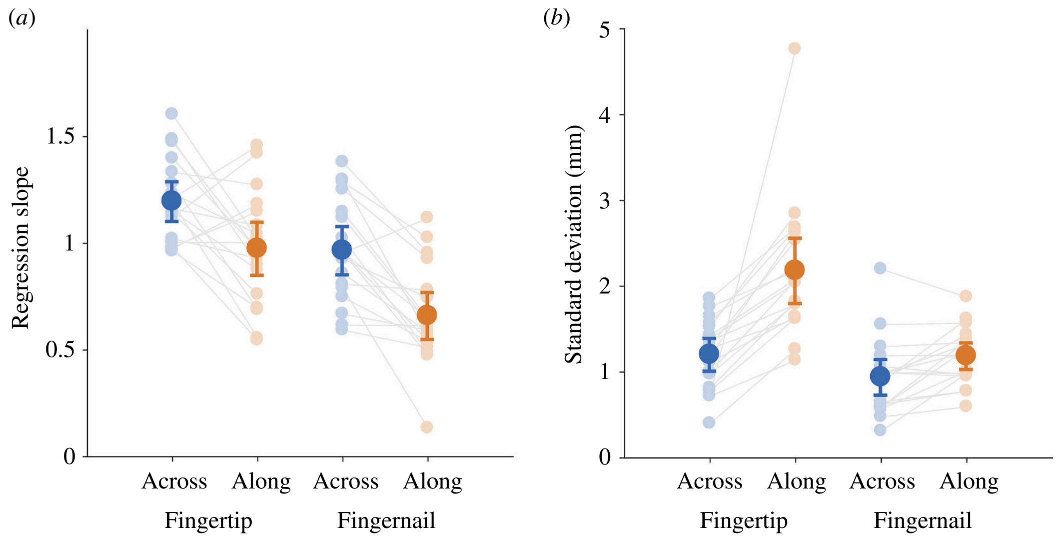

Figure 4. Results from experiment 1. (*a*) Mean slopes regressing judged stimulus location on the actual location in both orientations on the fingertip and fingernail. If participants were unable to localize touch, slopes should on average be 0. (*b*) Mean standard deviation of responses in each orientation averaged across the nine stimulus locations. Error bars are 95% CIs.

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, s.d.: 0.315), $t(18) = 11.60$, $p < 0.0001$, $d = 2.661$, and across finger width (*M*: 0.554, s.d.: 0.824), $t(18) = 2.93$, $p < 0.01$, $d = 0.673$. Performance was also well above chance levels on the fingernail, with regression slopes greater than 0 both along fingernail length (*M*: 0.680, s.d.: 0.235), $t(18) = 12.61$, $p < 0.0001$, $d = 2.893$, and across fingernail width (*M*: 0.756, s.d.: 0.304), $t(18) = 10.84$, $p < 0.0001$, $d = 2.486$. As in experiment 1, regression slopes on the fingernail were positive for all 19 participants in both orientations.

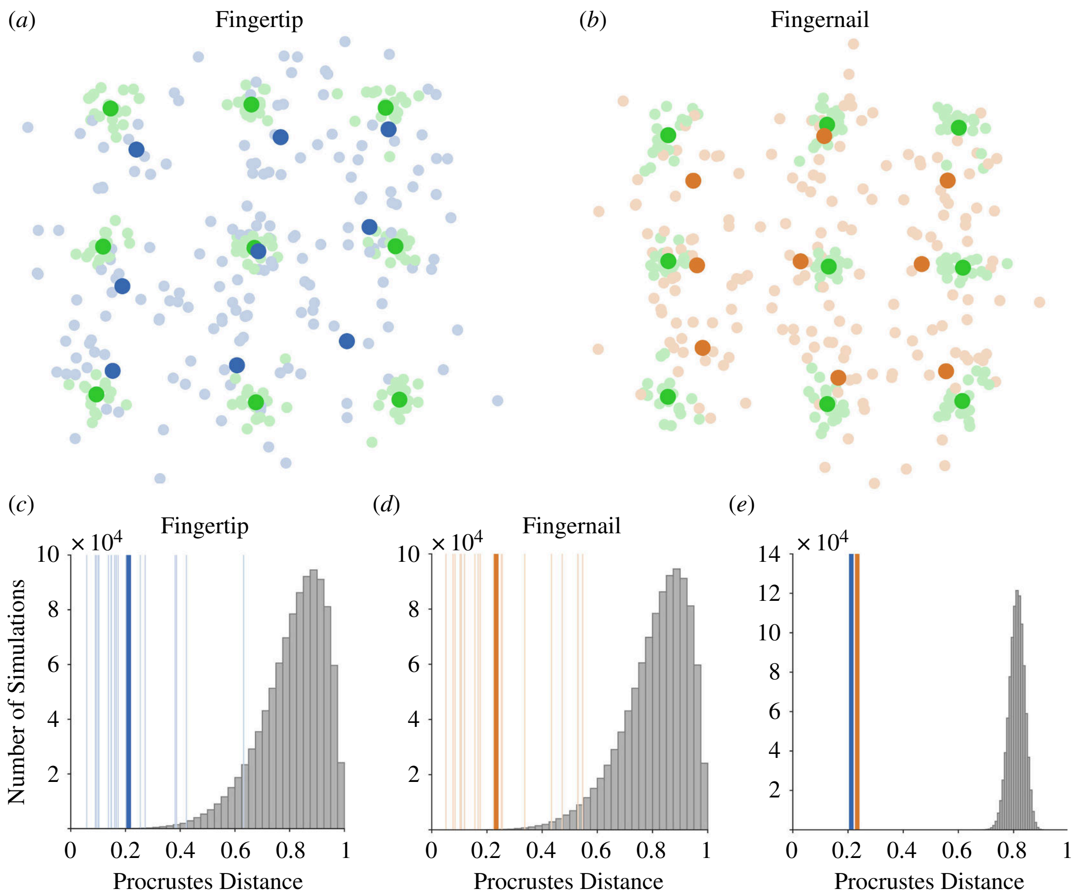

Figure 5. Results from experiment 2. (*a*,*b*) Maps of the nine actual stimulus locations (in green) and judged locations on the fingertip (in blue; *a*) and fingernail (in orange; *b*) placed into Procrustes alignment. Dark marks indicate grand means across participants while lighter marks show mean values for each individual participant. (*c*–*e*) Procrustes distances comparing perceptual maps to square grids on the fingertip (*c*) and fingernail (*d*). 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 (*c*,*d*) and from simulations of a sample of 19 participants (*e*).

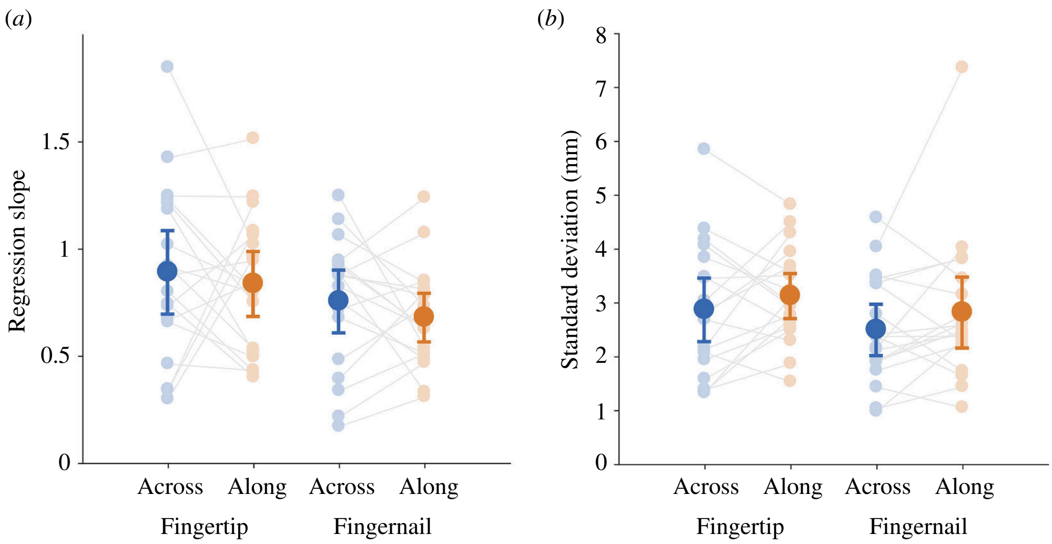

Figure 6. Results from experiment 2. (*a*) Mean slopes regressing judged stimulus location on the actual location in both orientations on the fingertip and fingernail. (*b*) Mean standard deviation of responses in each orientation averaged across the nine stimulus locations. Error bars are 95% CIs.

An ANOVA on regression slopes showed a marginally significant effect of body part, $F_{1,\,18} = 4.11$, $p = 0.058$, $\eta^2 = 0.186$; as in experiment 1, slopes were slightly higher on the fingertip than the fingernail. There was no significant effect of orientation, $F_{1,\,18} = 0.75$, $p = 0.397$, $\eta^2 = 0.040$, nor an interaction, $F_{1,\,18} = 0.04$, $p = 0.838$, $\eta^2 = 0.002$.

The right panel of figure 6 shows the standard deviation of responses in both orientations. An ANOVA showed no significant effects of body part, $F_{1,\,18} = 1.70$, $p = 0.209$, $\eta^2 = 0.046$, orientation, $F_{1,\,18} = 2.21$, $p = 0.155$, $\eta^2 = 0.033$, nor an interaction, $F_{1,\,18} = 0.05$, $p = 0.827$, $\eta^2 = 0.004$.

4. Discussion

This study shows that people can localize tactile stimuli applied to the fingernail. Localization 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 localize touch on the fingernails may be related to recent research, which has shown that people can localize touch applied to a stick that is held in the hand [32]. In both cases, the precise location of a stimulus is perceived despite the absence of any tactile receptor 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 those widely used by blind people [17,37–39]. The contribution of Miller *et al.* [32] was to show that it is not just that 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 that people can perceive touch applied to the distal extremity of the fingernail, as emphasized 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 by Miller *et al.* for passive touch applied to a long stick (mean slope: 0.57) [32].

Anatomical studies of mechanoreceptors in the nail bed have identified populations of SA 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 SA mechanoreceptors along the borders of the fingernail [23,24]. These SA responses, particularly SA-I fibres associated with Merkel cells, may underlie the precise spatial localization ability described in this study. SA-II responses associated with Ruffini endings may also be involved. A recent study showed that the intraneural stimulation of SA-II units in the fingernails produced clear experiences of pressure being applied to the nail [41]. Notably, however, Miller *et al.* [32] linked tactile localization 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 nail bed itself, these cells lie deep in 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 localization on the fingernail was more accurate and less variable in the medio-lateral finger axis than in the proximo-distal axis, at least for the middle finger in experiment 1. This is consistent with the pattern found at other locations on the dorsal surface of the hand in localization tasks [33,36], as well as in other tasks assessing spatial acuity [42,43], tactile distance perception [44,45] and proprioceptive localization judgements [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 localization of touch. While the functional implications of this ability remain uncertain, this finding is consistent with claims that 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.

Ethics. This research was approved by the School of Psychological Sciences Research Ethics Committee (approval no. 2223017).

Data accessibility. Raw data and the script used to run the study are available online [49].

Declaration of AI use. I have not used AI-assisted technologies in creating this article.

Authors' contributions. M.R.L.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft.

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