THE COARSE MENTAL MAP OF THE BREAST IS ANCHORED ON THE NIPPLE

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ABSTRACT

Touch plays a key role in our experience of our body and our interactions with the world, from the objects we manipulate to the people we touch. While the tactile sensibility of the hand has been extensively characterized, much less is known about touch on other parts of the body. Despite the important role of the breast in nursing as well as in affective and sexual touch, little is known about its sensory properties. To fill this gap, we investigated the spatial acuity of the breast and compared it to that of the hand and back, body regions that span the range of tactile spatial acuity. First, we found that the tactile acuity of the breast was even lower than that of the back, heretofore the paragon of poor acuity. Second, acuity was lower for larger breasts, consistent with the hypothesis that innervation capacity does not scale with body size. Third, touches to different regions of the nipple were largely indistinguishable, suggesting that the nipple is a sensory unit. Fourth, localization errors were systematically biased toward the nipple and more so at greater distances from the breast.

INTRODUCTION

The sense of touch fulfills a variety of different functions in everyday life, from guiding our interactions with the environment to supporting affective communication and sexual function (McGlone et al., 2014). One of the key properties of touch sensations is that they are localized to a specific part of the body: contact on the shoulder produces a sensation experienced on the shoulder, for example. The precision with which we can localize events on the skin has been shown to be determined by the innervation density at that skin location (Corniani & Saal, 2020; Craig & Lyle, 2001). Because the skin of the fingertips and lips is the most densely innervated, the acuity of these body regions is highest, conferring to us an enhanced ability to distinguish touches on the fingers and lips even if they are close to each other. Innervation density is in part determined by the functional role of different body parts: the fingertips are densely innervated because they account for the vast majority of contacts with objects, and precise information about object interactions is critical to dexterous manipulation (Johansson & Vallbo, 1979). In contrast, the acuity on the back is low because precise localization of a touch on the back is of no use under most circumstances. Innervation density is not only determined by the function of different body regions but also by body size. For example, people with large hands exhibit lower acuity than those with small ones (Peters et al., 2009; Wong et al., 2013). This phenomenon is hypothesized to reflect the fact that the number of nerve fibers does not scale with body size: A large body will be more sparsely innervated than a small one given a fixed number of nerve fibers.

While tactile acuity has been extensively studied on the limbs and face, acuity on the torso has received far less experimental attention and has been restricted to one or two locations (Mancini et al., 2014; Weinstein, 1968). To fill this gap, we sought to characterize the spatial acuity of the female breast, whose role in nursing, affective touch, mediating the feel of a hug, and sex, as one of the principal erogenous zones, sets it apart from other regions of the body. In previous studies, the tactile acuity of the breast has been found to be comparably low to that of the back and calf (Weinstein, 1968). However, the experimental approaches were outdated and susceptible to inaccuracies (Craig & Johnson, 2000), only the outer breast was tested (to the exclusion of the nipple-areolar complex), and the relationship to breast size was not assessed. Given that breasts grow to vastly different sizes, and do so late in life, after the nervous system is nearly fully developed (Javed & Lteif, 2013), the female breast offers a powerful test of the fixed innervation hypothesis, which would predict that women with large breasts would have poorer spatial acuity than women with small ones.

In the present study, we first measured the tactile acuity of two regions of the breast – the outer breast and medial breast, which includes the nipple-areolar complex (NAC) –, and compared these to their counterparts on the hand and back. Second, we examined the relationship between the acuity of the outer breast and breast size. Third, we examined women's ability to judge the absolute location of touches to their breast. First, we found that the spatial acuity of the breast is very low, far lower than that on the hand and even lower than that on the back. Second, spatial acuity decreases with breast size, as predicted from the fixed innervation hypothesis. Third, touches to different parts of the nipple are nearly indistinguishable, suggesting that the nipple is a sensory unit. Fourth, touches on the outer breast are mis-localized systematically as being nearer to the nipple than they actually are.

RESULTS

Location discrimination is poorer on the breast than on the hand and back

First, we measured the subjects' ability to judge the relative position of two touches applied in rapid succession at two nearby locations on the skin using a punctate probe. The first of the two touches, the reference, was at the same position on each trial, and the second touch, the test, was either above or below the first, at a pre-specified distance. For the hand, distances ranged from 1 to 10 mm; for the other body regions, distances ranged from 2.5 to 40 mm, anticipating lower acuity and based on preliminary testing (Figure 1). The subjects' task was to report whether the test was located above or below the reference. We then assessed the subjects' performance as a function of the distance between the test and reference.

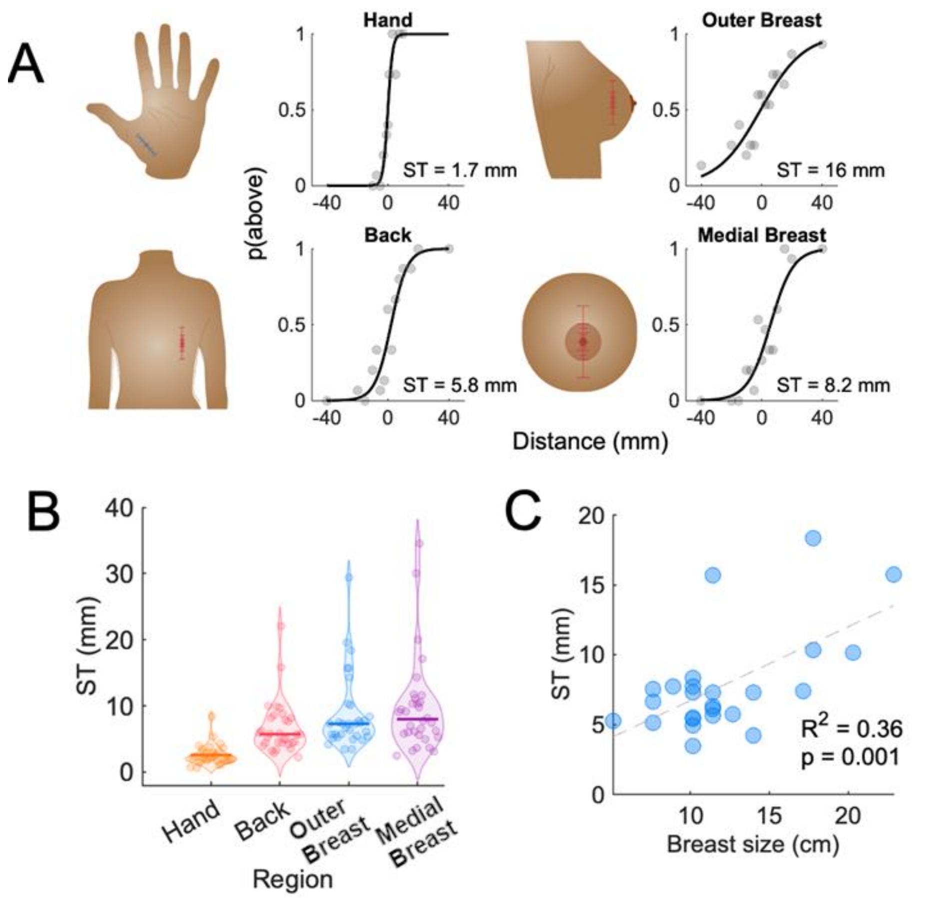

Figure 1. Location discrimination. A| Performance of one subject on the location discrimination task for the hand, back, outer breast, and medial breast (with NAC). Negative values denote test points "below" the reference. The spatial thresholds (ST), estimated from the fitted psychometric function, denotes the distance at which the subject could correctly judge whether a touch was above or below the reference 75% of the time. The spatial layout is shown on each body region to the left of the corresponding psychometric function. For the hand, the farthest point was 10 mm away from the reference. For other body regions, it was 40 mm away. B| Distribution of spatial thresholds for the hand, the back, the outer breast, and the medial breast. The hand is the most acute and the outer breast and medial breast are the least. Circles denote the STs of individual subjects and lines denote medians across subjects. C| Spatial acuity of the breast as a function of breast size, gauged by bust minus under-bust. Women with larger breasts exhibit lower spatial acuity on the breast. (N=32)

As expected, the psychometric functions were steeper for the hand than for the back (Figure 1A). That is, to yield equivalent discrimination performance, the reference and test points needed to be farther apart on the back than on the hand. Interestingly, the outer breast and medial breast yielded even shallower functions than did the back. As a measure of spatial acuity, we estimated from the psychometric function for each subject and body location the distance between reference and test that yielded 75% correct discrimination performance, the spatial threshold (ST). Spatial thresholds were lowest for the hand (mean ± standard deviation = 2.5 ± 1.4 mm), intermediate for the back (6.6 ± 3.9 mm), and highest for the outer breast and medial breast, which included the NAC (8.7 ± 5.6 mm, 9.7 and ± 7.1 mm, respectively) (Figure 1B). In other words, touches needed to be nearly 4 times as far apart on the breast than on the hand to yield equivalent location discrimination performance. The STs were significantly lower for the hand than for the other locations (mean ranks: 1.1, 2.7, 3.0, and 3. 3; randomization test, $p < 0.001$), STs were significantly lower for the back than for the NAC ($p < 0.005$) but not the breast ($p = 0.09$), and STs for the breast and NAC were not significantly different ($p = 0.07$).

Tactile acuity is worse for women with larger breasts

The differences in ST across body locations were dwarfed by differences across subjects. The most sensitive subject was almost ten times more acute than the least sensitive subject. The spatial acuity of the hand has been shown to depend on the size of the hand, with smaller hands yielding better acuity (Peters et al., 2009). With this observation in mind, we investigated whether the inter-subject differences in breast acuity might be driven in part by differences in breast size. We found that, indeed, ST increased significantly with breast size – estimated by measuring the difference between the bust (circumference of the torso at the nipple line) and under-bust (circumference of the torso at the inframammary fold). Specifically, women with larger breasts exhibited a significant tendency to have lower spatial acuity ($R^2 = 0.36$, $p < 0.01$, Figure 1C). To verify that the association between acuity and breast size was not spurious, we examined the relation between breast size and STs for the hand, back, and medial breast and found there was none ($p > 0.05$, Supplementary Figure 1)

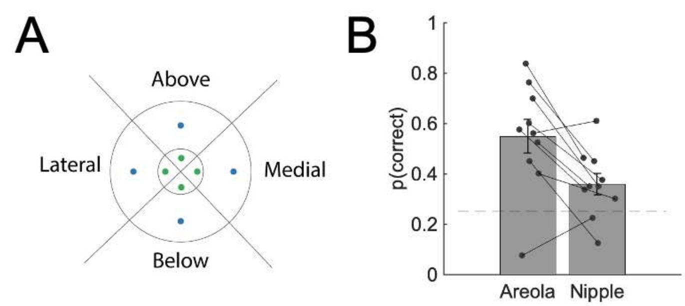

Figure 2. Spatial acuity of the nipple and areola. A| Test locations for the quadrant discrimination task. The subject reported location using a number from 1 to 4 progressing clockwise from "above." B| Proportion correct localization. (N=10)

The nipple is a unit

STs obtained from the medial breast are difficult to interpret because they reflect judgments about three anatomically distinct regions of the breast: the nipple, the areola, and the nearby outer breast. To assess the acuity within the nipple and areola separately, we delivered a punctate touch to a location at one of four quadrants on the nipple or areola and the subject reported the quadrant in which the touch had been delivered (Figure 2A). We could then assess the degree to which different regions of these breast components were distinguishable from one another. We found that subjects could report which of four quadrants was touched on the areola, as evidenced by above chance performance (χ^2 test on proportion correct greater than chance, $p < 0.01$), but their performance was relatively poor. The one outlier systematically misperceived the location. Subjects performed even more poorly in identifying the quadrant of a touch on the nipple, with only five out of ten achieving above chance performance (Figure 2B). In other words, while touches to different parts of the areola are somewhat distinguishable, the nipple is a sensory unit with little to no differentiation.

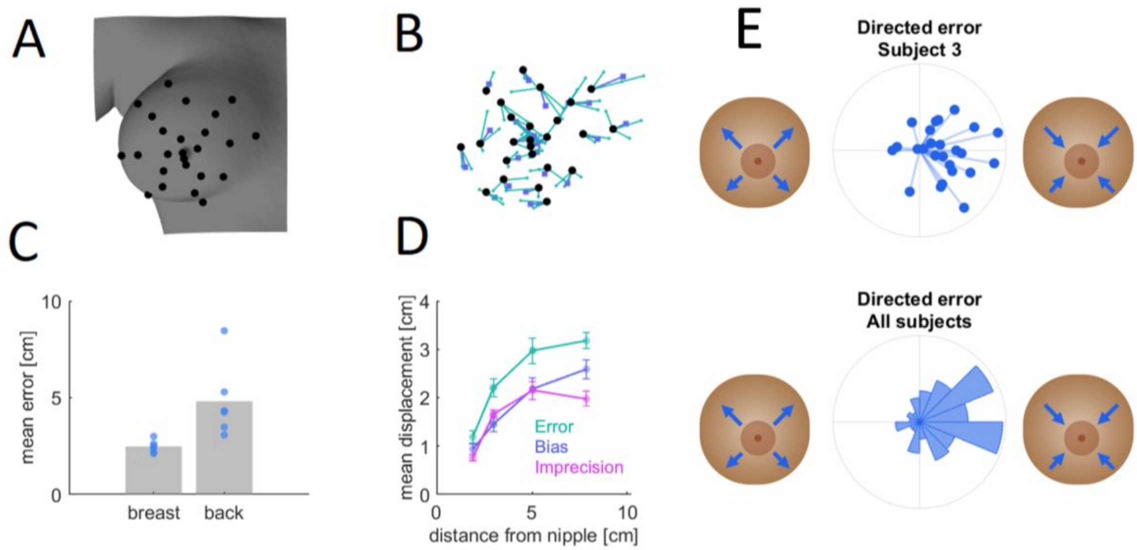

Figure 3. Absolute localization task. A| Example of a three-dimensional rendering of the breast of one of the participants. Black points denote the actual locations of the 25 touches. B| Actual and reported locations of the touches. Teal points denote reported location and blue points are the centroids of the reported locations. C| Mean localization error for the back and the breast. Blue dots show each participant, and the grey bar shows the mean error across participants. D| Mean error, bias, and imprecision averaged across participants. Error bars denote SEM. E| Perceived location is biased toward the nipple. Top: The polar coordinate denotes the angle between the true and reported location, normalized to the nipple. An angle of zero corresponds to a displacement of the perceived location directly toward the nipple. The radial coordinate denotes the magnitude of the error. Bottom: Polar histogram of error angle with respect to the nipple for all participants. (N=6)

Absolute localization on the breast is anchored to the nipple

In the experiments described above, we investigated subjects' ability to distinguish the relative locations of two touches to the breast. Next, we examined their ability to identify the absolute location of a touch on their torso. To this end, we presented a single touch to the breast or the back with a punctate probe at one of 25 locations and each subject marked the location of the touch on a three-dimensional digital image of her own breast or back (obtained using EM3D, Brawny Lads Software, LLC.)(Figure 3A,B).

We found that the absolute magnitude of the errors on the breast (mean ± standard deviation = 2.5 ± 0.3 cm) were significantly smaller than those on the back (4.8 ± 1.9 cm), ($t(10) = 2.9101$, $p < .05$) (Figure 3C). Thus, the absolute localization task and location discrimination task yielded discordant results about the relative acuities of the breast and back: according to the location discrimination task, the back demonstrates higher spatial acuity than the breast, but according to the absolute localization task, accuracy of localization is greater on the breast than the back. However, in the discrimination task, STs are relatively impervious to systematic biases and instead reflect accuracy in a comparison. In contrast, errors in absolute localization can be caused by poor precision across multiple attempts at localizing the same point or by systematic biases, of precisely reporting an incorrect location. With these principles in mind, we examined whether the observed errors in absolute localization judgments reflected poor precision or systemic biases in perceived location. To this end, we computed the absolute distance between the centroid of the perceived location (across three trials) and the actual location of the stimulus. A bias would cause perceived locations to be systematically displaced relative to the actual location; poor precision would cause perceived locations to be distributed widely but randomly around the actual location.

We found that errors could be attributed to both bias and imprecision, and that all errors increased systematically with distance from the nipple (Figure 3D, green line). Next, we investigated whether the bias was significantly greater than would be expected by chance. To this end, we allocated to each error a random angle around the actual location and recomputed the bias and imprecision for these simulated data (Supplementary Figure 2), which reflect the level of bias and imprecision one would expect if all errors were simply due to imprecision. We found that the measured bias was significantly greater than its simulated counterpart (Figure 3D), demonstrating that the perceived location of a touch on the breast was systematically biased. Next, we examined whether the biases were systematic in their direction by computing the angle between each location judgment and the actual location (Figure 3E). We found that these biases were systematically directed toward the nipple and significantly so for all but one subject (Supplementary Figure 3). Thus, the perceived location of a touch on the outer breast is pulled toward the nipple, and more so at greater distances from the nipple.

In contrast, localization errors on the back were even more dominated by bias than were those on the breast (Supplementary Figure 4). Indeed, subjects were consistent in perceiving touches as being closer to the shoulder than they actually were (Supplementary Figure 5). The imprecision was higher on the breast than on the back, consistent with the results from location discrimination task.

DISCUSSION

First, we found that the spatial acuity of the outer breast – excluding the nipple and areola – is almost four times lower than that of the hand, even lower than that of the back, previously considered the epitome of poor acuity. The nipple is essentially a sensory unit, as touches to different aspects of the nipple are nearly indistinguishable from one another. The areola is intermediate in sensitivity between nipple and outer breast. Second, the acuity of the breast tends to be poorer for women with large breasts, consistent with the theory that innervation capacity is fixed, leading to an inverse relationship between size and acuity. Third, the nipple constitutes a landmark on the breast, as evidenced by the fact that absolute localization judgments are less accurate and more biased for touches that are far from the nipple and perceived location is pulled systematically toward the nipple.

The poor spatial acuity of the breast

The poor spatial acuity of the breast – about four times lower than that of the hand and comparable to that of the back – replicates previous findings (Weinstein, 1968), though these used less reliable methods – two point threshold and a 'same-different' paradigm. Tactile spatial acuity is determined by density of innervation, though more neural tissue is devoted to more highly innervated body regions and this increased central representation is a key contributor to the increased acuity. The breast is primarily innervated by intercostal nerves III to V, which comprise medial and lateral branches. We compared the magnitude of the absolute localization errors on the medial and lateral aspects of the breast and found no difference (Supplementary Figure 6), suggesting that the two branches confer to the breast comparable acuity. That imprecision was greater in the outermost aspects of the breast suggests that the innervation is sparser there than around the nipple. The low spatial acuity of the nipple and areola is consistent with a histological study revealing these to be sparsely innervated (Gutiérrez-Villanueva et al., 2020).

Larger breasts confer lower acuity

We found a significant relationship between breast size and spatial acuity: women with larger breasts tended to exhibit lower spatial acuity on their breasts, consistent with previous findings that tactile acuity scales with body size. Indeed, the spatial acuity of the hand has been shown to depend on the size of the hand, with smaller hands exhibiting better acuity (Peters et al., 2009; Wong et al., 2013). These results are consistent with the hypothesis that the number of tactile nerve fibers does not scale with body size, so fibers are more sparsely distributed on bigger bodies, leading to lower acuity.

The nipple is a landmark

The mental representation of the body is not uniform and veridical (Longo, 2022). Localization tends to be more precise when stimuli are applied near anatomical points of reference that form perceptual anchor points (Weber, 1834). For example, the navel and spine act as anchor points along the abdomen (Cholewiak et al., 2004; Van Erp, 2005): touches to the navel or spine are never mistaken for touches anywhere else on the abdomen. Furthermore, touches to locations near these two anchor points are mislocalized following a bias toward these areas: touches near the navel are pulled toward the navel and touches near the spine are pulled toward the spine. Similar biases are observed on the back of the hand, where touches are mislocalized to be nearer the fingers than they actually are (Mancini et al., 2011), and on the forearm, where they are pulled toward the wrist (Fuchs et al., 2020). Analogously, we found that acuity is highest near the nipple, and perceived locations are pulled toward the nipple, consistent with the nipple acting as an anchor point on the breast. On the back, the shoulder acts as an anchor point (Supplementary Figure 4).

Conclusion

The breast has unique sensory properties because (1) it mediates nursing, (2) it comprises distinct components – the nipple, areola, and outer breast –, which differ in the type of skin and patterns of sensory innervation, (3) it gives rise to erogenous sensations, and (4) it undergoes variable expansion across individuals during puberty. First, we find that spatial acuity on the breast is worse than that of the back, previously regarded as the body region with lowest tactile acuity. Second, spatial acuity is worse in larger breasts, presumably due to sensory innervation being fixed prior to expansion during puberty. Third, the nipple itself is perceived as a single spatial unit but serves as an anchor for the mental map of the breast.

Methods

Participants

A total of 48 healthy adult women (24.2 ± 3.1, 19-32 years) participated in this study: Thirty-two in the location discrimination task (mean ± standard deviation, age range; 22.6 ± 2.7, 19-28 years), ten in the medial breast quadrant localization task (25.3 ± 3.8, 19-32 years), and six in the absolute localization task (24.7 ± 2.9, 20-28 years). Experimental procedures were performed in accordance with the relevant guidelines and regulations and were approved by the Institutional Review Board of the University of Chicago (IRB 18-0135). Informed consent was obtained from each subject, and the subjects were compensated for their participation. We excluded any women who were currently pregnant or breastfeeding, had had breast surgery, or had any neurological illness.

Breast measurements

In addition to self-reported bra size, we collected standardized, objective measurements that represented breast size beyond the overall size of the participant. For this, we measured the bust – i.e. the circumference of the chest at the level of the nipple (bust) – and subtracted from it the under-bust, the circumference at the level of the inframammary fold (mean ± standard deviation, range; 12.4 ± 4.6, 7.6-25.4 cm). We also measured the diameter of the areola and nipple (areola: 37.4 ± 11.9, 21-80 mm; nipple: 12.7 ± 2.7, 7-20 mm).

Tactile Stimuli

Touches were delivered manually with an XP-Pen, whose tip has a diameter of 1 mm. The experimenter lightly pressed the stimulus against the skin, ensuring that the skin was indented uniformly across touches. The participants were asked to report any discomfort with the application of the stimulus or the inability to feel the application of the stimulus reliably. Note that spatial acuity is pretty consistent across stimulus amplitudes as long as the touch is sufficiently above threshold (Gibson & Craig, 2002), which was the case here.

Psychophysical tasks

<u>Location discrimination</u>

Acuity was tested at each of four body regions: the lateral breast, the medial breast (which includes the NAC), the thenar eminence of the hand, and the upper back. The subject – wearing a gown that exposed only the location to be tested – lay on her back on a massage table for testing on the lateral breast, medial breast, and thenar eminence, and on her stomach for the testing on the back. Unless the subject expressed a preference, the side of the body to be tested (left/right) was chosen randomly (and counterbalanced) but each subject was tested on one or the other side for all regions. The order in which the different regions were tested was counterbalanced to eliminate any effects of fatigue or learning.

On each trial, two touches were applied to nearby locations and the subject's task was to indicate whether the second touch was above or below the first by pressing one of two buttons on a keypad. The location of one of the two touches (the reference) was consistent across each experimental block and the location of the second (the comparison) varied from trial to trial (each at a pre-specified distance). Fifteen comparison locations, aligned along an axis parallel to the body's axis, were tested on the back, lateral breast, and medial breast. Touch locations were drawn on the body to ensure repeatable presentation and comparisons were located placed 0, 2.5, 5, 7.5, 10, 15, 20 or 40 mm above or below the reference (Fig. 1). Each comparison was repeated five times per block over three blocks (for a total of 15 repeats per comparison, with 225 total trials per body region) in a randomized order. Thirteen comparison locations were tested on the hand, 0, 1, 3, 6, 7.5, and 10 mm away from the reference in both directions along an axis in line with the thumb (Fig. 1) For the hand, a judgment of "above" indicated the comparison was displaced toward the thumb relative to the reference. Each location was repeated 5 times across three experimental blocks (for a total of 15 repeats per comparison, with 195 total trials).

Performance was gauged by the proportion of times the subject judged a comparison as above the reference as a function of distance from the reference, where negative distances indicate comparison locations below the reference. Psychometric functions were fit to the data and used to compute the inter touch distance that yielded 75% correct judgments (the spatial threshold, ST).

<u>Quadrant discrimination</u>

The objective of this experiment was to assess the degree to which women can distinguish touches to different parts of their NAC. On each trial, the subject was touched at one four locations on the nipple or areola (organized in a quadrant) and verbally identified the touch location using a number from 1 to 4 (Figure 2A). Each location was touched ten times per block (40 trials per block, with 80 total trials per breast region). For the areola, each touch was located halfway between the edge of the areola and the nipple. For the nipple, each touch was delivered at the edge of the nipple, in line with each point on the areola (Figure 2A). The testing side was chosen randomly for each subject (6 left/4 right).

<u>Absolute localization</u>

The objective of this experiment was to gauge the accuracy with which women can report where on their breast or back a touch was delivered. On the breast, touches were arranged such that the nipple was the central point and other touches radiated outwards from it (Supplementary Figure 5). On the back, touches were arranged the same way around a central point located on the shoulder blade. First, the subject's skin was marked, then a three-dimensional scan of the breast or back was obtained using the EM3D application (Brawny Lads Software, LLC.) and uploaded to Blender. The surface of the breast was then masked with a uniform layer of grey to obscure the makings. A laptop was positioned such that the subject could touch the monitor to report where the touch was experienced on the 3D rendering of her breast. Each of the 25 locations was touched in a pseudorandomized order while the subject closed her eyes. After the touch, the subject marked the perceived location of the touch on the 3D rendering of her breast or back using a laptop. The subject was encouraged to manipulate the 3D model freely to obtain the best view of her breast or back on each trial. Reported locations accumulated on the 3D model throughout the block (during which each location was touched once.) but were removed at the start of each of three blocks (yielding a total of 3 repeats for each of the 25 locations).

Data Analysis

Spatial threshold. To quantify the spatial acuity at each test location, we fit a psychometric function to the probability of judging the second touch as above the first vs. the relative location of the two stimuli. From these functions, we estimated the distance above and below the reference location at which the subject would respond correctly 75% of the time and took the mean of these distances to obtain the spatial threshold (ST). The ST is the distance two touches need to be from each other to be able to reliably judge their relative locations.

Error and bias in the absolute localization task. We first computed the distance between the actual location of the touch and the location reported by the participant on the 3D representation of the breast (in Blender). We then computed the centroid of all reported locations for each actual location. To the extent that judged locations were systematically displaced from the actual location, the centroid would be displaced relative to its corresponding actual location. We then computed two error metrics. First, we computed the distance of each reported location from its corresponding centroid to gauge imprecision: Reporting different locations upon repeated touches to the same location would lead to high imprecision. Second, we computed the distance between each centroid and its corresponding actual location to gauge bias: Systematic errors would lead to high bias. All errors were normalized by each subject's cup size before averaging across subjects to eliminate any effect of breast size on error magnitude. We assessed the significance of the bias term by performing a Monte Carlo simulation, wherein we sampled the measured absolute errors and distributed them randomly around the actual location, then computed the imprecision and bias metrics for these simulated data. To the extent that biases could be attributed to imprecision, the magnitude of the biases in the simulated data would match those in the actual data.

DATA AVAILABILITY

The data used in the current study will be made available by the corresponding author on reasonable request.

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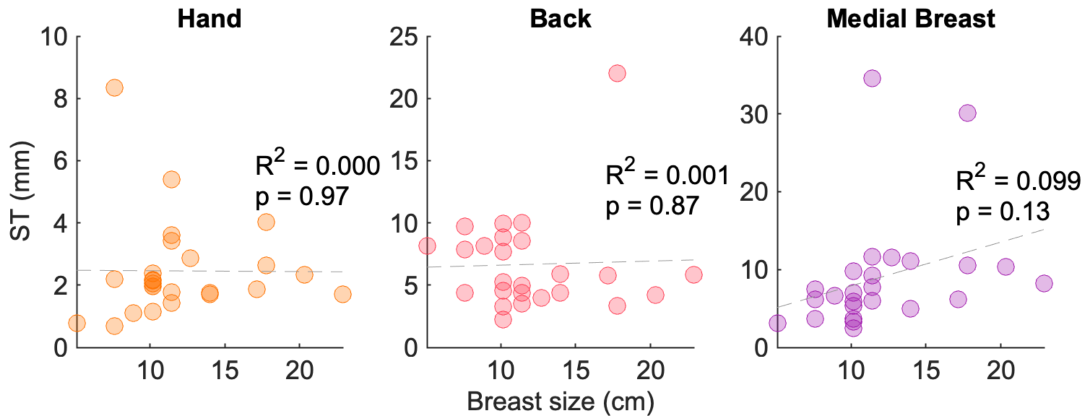
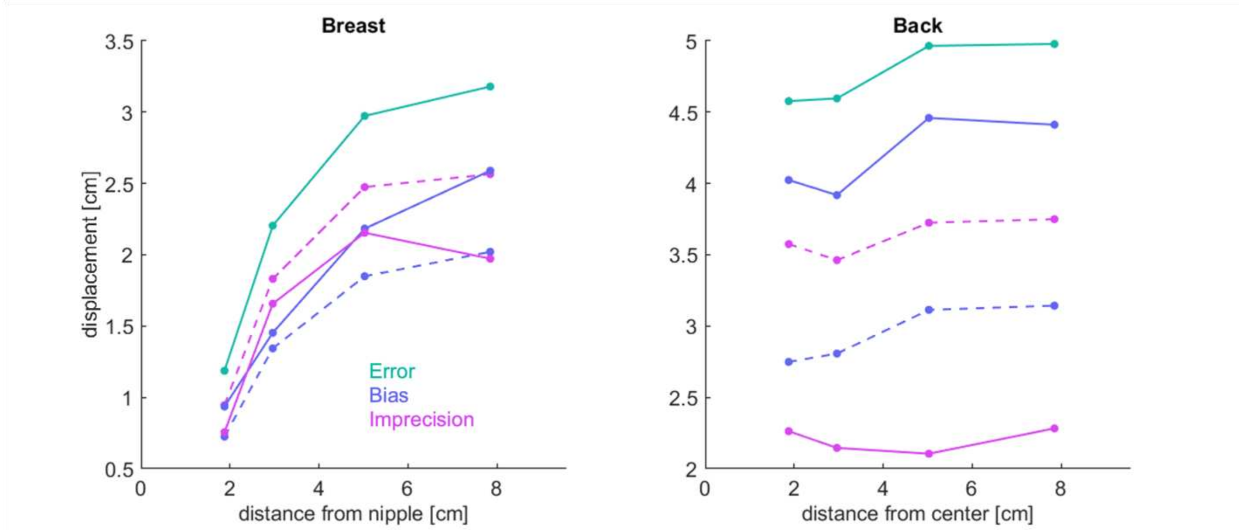
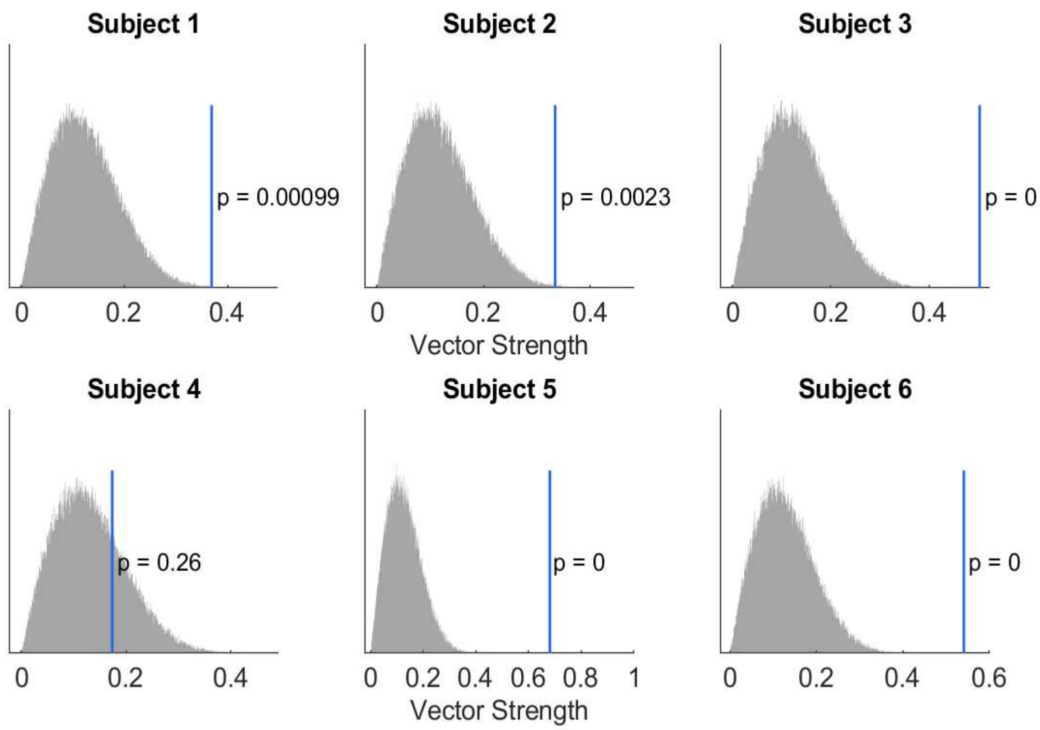
SUPPLEMENTARY FIGURES



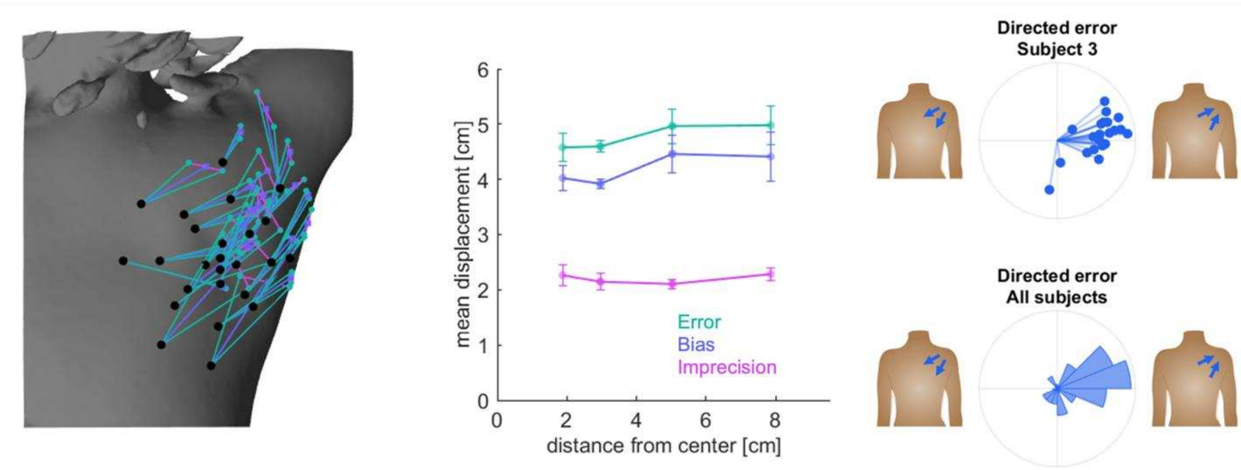
Supplementary Figure 1. ST for the hand, back, and medial breast vs. breast size, measured by subtracting the under-bust from the bust, along with the best fitting line.



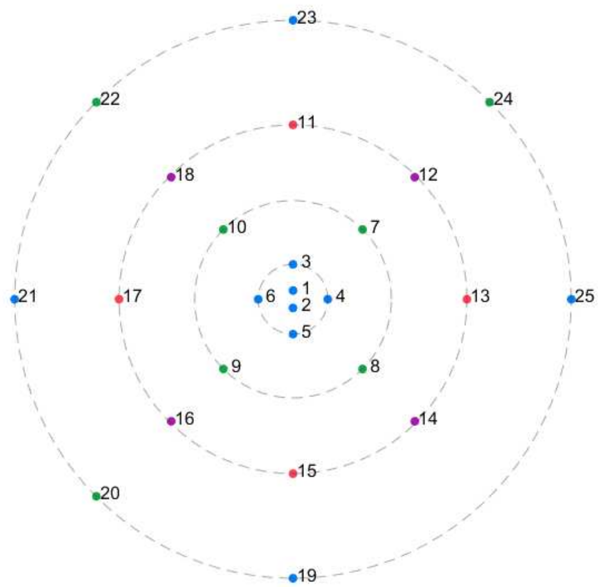
Supplementary Figure 2. Monte Carlo simulations of bias and imprecision for the breast and the back. Dotted lines show the simulated data. For both body regions, the measured bias is significantly higher than would be expected if it simply reflected imprecision. Conversely, the imprecision is significantly lower than expected since the overall error remains constant. We conclude that the subjects' errors reflect both bias and imprecision.



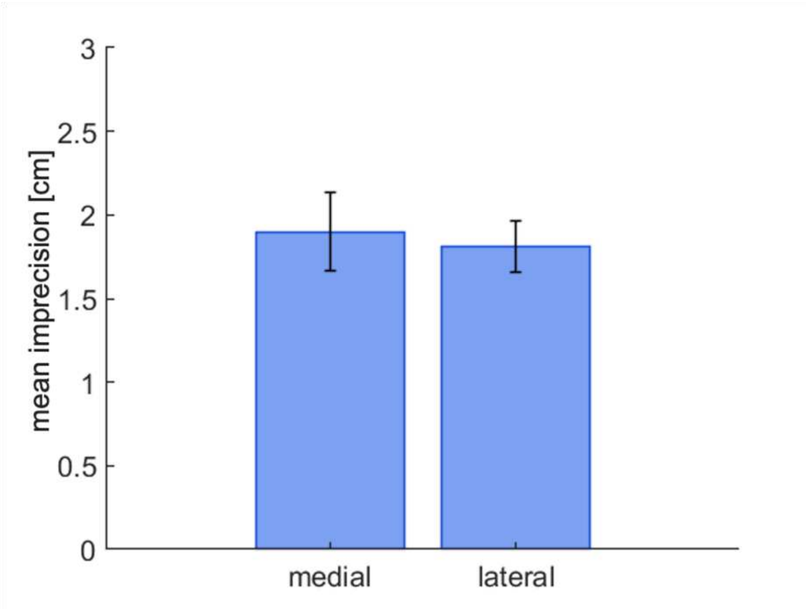
Supplementary Figure 3. Localization biases are consistent across locations. Histograms showing the Monte Carlo distributions of vector strength one would expect if reported locations were randomly distributed around the actual location. Blue lines show the measured vector strength for each participant, along with the proportion of times the vector strength for shuffled errors exceeded the measured value.



Supplementary Figure 4. Absolute localization performance on the back. A| An example of a three-dimensional rendering of the back of one of the participants. Black points represent the actual locations; cyan points the reported locations; magenta points denote the centroid of the reported locations. Each reported location is connected by a magenta line to its centroid and by a cyan line to its actual location. Centroids are connected by a purple line to their corresponding actual location. B| Errors as a function of distance from the centroid of all points. Most of the error in the back is driven by bias, rather than imprecision (more so than on the breast). C| Perceived location on the back is systematically biased towards the shoulder. Top: Polar plot of perceived locations of stimuli for one representative subject, with angles normalized to the shoulder: 0^o denotes the direction toward the shoulder. Bottom: Polar histogram of all perceived points across participants, normalized to the shoulder.



Supplementary Figure 5. Absolute localization: Location of the 25 touches. Points 1 and 2 are centered on the nipple.



Supplementary Figure 6. Imprecision of perceived location – the distance between each reported location and their respective centroid – on the medial and lateral aspects of the outer breast. Both aspects are equally acute, implying equivalent innervation densities.