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Skin Stretch Modulates Tactile Distance Perception Without Central Correction Mechanisms

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Tactile distance perception is influenced by stimulus orientation. On the hands or face, effects of orientation may originate from the mostly oval shape of receptive fields (RF) of which the long axis aligns with the proximodistal body axis. As tactile distance estimation relies on the number of RFs between stimuli, their alignment leads to a distortion of perception with distances being perceived as shorter in the proximodistal than the mediolateral body axis. It is however unknown, how physical manipulations such as skin stretch affect distance perception. Participants judged which of two distances aligned with the mediolateral or proximodistal axis on their dorsal dominant hand felt larger in two conditions: without physical manipulation and with proximodistal skin stretch. Distances were perceived shorter in proximodistal direction in both the nonstretch and the stretch condition, which was significantly pronounced in the stretch condition. Skin stretch led to perception of tactile distances as smaller, possibly related to the removal of afferent nerve endings and corresponding somatosensory RFs in the same external reference frame between the two touches. Though skin stretch is represented centrally, our results likely show that no correctional top-down mechanism corrects for skin stretch when estimating tactile distances.

Public Significance Statement

We show that skin stretch affects tactile distance perception on the back of the hand with tactile distances being perceived as shorter on stretched than on nonstretched skin. Most likely, no correctional top-down mechanism corrects for skin stretch when estimating tactile distances.

Keywords: tactile distance perception, somatosensation, skin stretch

Supplemental materials: https://doi.org/10.1037/xhp0001063.supp

The repertoire of our somatosensory abilities defines many ways in which we interact with the world. Our largest organ, the skin, is equipped with manifold receptors and sensory afferents to detect a broad spectrum of sensations, from the hazard of noxious heat to the pleasant feeling of gentle strokes (Lumpkin & Caterina, 2007). Moreover, the skin, together with muscles and joints, contributes to the perception of self-movement and self-position (i.e., kinesthesia and statesthesia), which is essential for our ability to maneuver our body and limbs in space and interact with our surroundings with targeted movements (Proske & Gandevia, 2012).

As one of the many somatosensory capabilities, we are able to determine the distance between multiple tactile stimuli (ten Donkelaar et al., 2020). Our perception of tactile distance, however, is subject to a variety of illusions and distortions, depending on various factors such as body part or stimulus orientation. Weber (Ross & Murray, 1996) had already observed in the 19th century that tactile stimuli felt further apart in body regions with low spatial sensitivity of the skin compared to body regions with higher spatial sensitivity. That means, the same tactile distance is perceived as larger on a more sensitive skin area, such as the hand, than on a less sensitive skin area, such as the back, an effect now known as Weber's illusion. Tactile distance perception also varies within the same body part depending on the orientation of stimuli. Most of the studies investigating this so called anisotropy have focused on

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The study was not preregistered. The data and analysis code that support the findings of this study are available online (https://doi.org/10.5281/zenodo.6385080).

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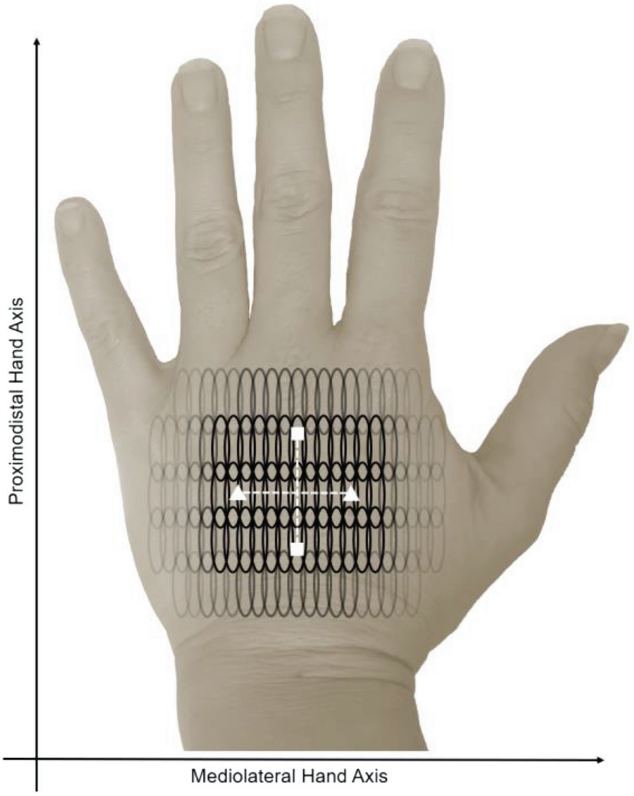
the hands (Fiori & Longo, 2018; Green, 1982; Knight et al., 2014; Longo, 2020; Longo & Haggard, 2011; Longo & Sadibolova, 2013), however, a distortion of tactile distance perception depending on stimulus orientation has also been found on the feet and legs (Green, 1982; Manser-Smith et al., 2021; Stone et al., 2018), the arms (Green, 1982; Knight et al., 2014) and the forehead (Fiori & Longo, 2018; Longo et al., 2015, 2020; Mainka et al., 2021) with tactile distances being perceived as larger when oriented in the mediolateral than in the proximodistal body axis.

These findings can neurophysiologically be explained by the geometry and spatial organization of receptive fields (RF). Usually, RFs relating to tactile afferents are shaped elliptically (Alloway et al., 1989; Brown et al., 1975; Fuchs & Brown, 1984) and their short axis is aligned with the mediolateral body axis (Brooks et al., 1961; Mountcastle, 1957; Powell & Mountcastle, 1959). According to the pixel model, tactile space can be seen as a two-dimensional grid, whereby each RF represents one pixel. The estimation of distances between two tactile stimuli on the skin would involve the count of pixels between the stimulated locations (Longo & Haggard, 2011). Therefore, with more RFs aligned in the mediolateral than in the proximodistal body axis, tactile distances are perceived as larger in the mediolateral body axis—or shorter in the proximodistal body axis (see Figure 1).

Despite the large body of knowledge that has been acquired around somatosensation in the past decades, there are still many open questions. For example, it has been recognized that not only ‘classic’ somatosensory stimuli like touch or heat can elicit stimulus responses, but also more ‘unorthodox’ physical stimuli like skin stretch (Edin, 1992, 2004; Grill & Hallett, 1995; Hulliger et al., 1979; Knibestöl & Vallbo, 1970). Additionally, skin stretch contributes to the perception of joint movement, which underlines the importance of cutaneous afferents in kinesthesia (Collins et al., 2005; Edin, 2001; Edin & Abbs, 1991; Moberg, 1983).

There is thus evidence that information about skin stretch is coded in the somatosensory cortex. It is unknown, however, whether and how this information is used to correct for changes in the spatial relations between locations on the skin when it stretches. One previous study investigated tactile size estimation on the lips when the participants either smiled broadly (i.e., stretched lips) or pouted their mouth (i.e., crimped lips). Interestingly, they found no evidence for size consistency in tactile distance estimation between those two conditions (Anstis & Tassinary, 1983). Another intriguing piece of evidence comes from a study of an achondroplastic patient who underwent surgical elongation of her arms (Cimmino et al., 2013). Tactile distance perception was measured both before and after her surgery by asking her to compare tactile distances on her arm and on her neck. Before her surgery, her performance on this task was similar to that of controls. In contrast, after the surgery, she showed a clear bias to underestimate distances on the arm. This suggests that her somatosensory cortex had not taken the surgically induced stretch of the skin into account in judging distance. That is, two skin locations which are 5 cm apart after arm elongation, would have been closer together before the surgery. If the somatosensory system continues to use an outdated representation of the spatial layout of the skin, the distances after elongation should underestimate true distance, exactly as found. Interestingly, one year after her surgery, her performance had shifted about halfway back to her presurgery level. This suggests that metric changes as a result of skin stretch can be accounted for, but that this may involve an extended process of long-term learning.

Figure 1
Tactile Distance Perception According to the Pixel Model



Note. The elliptical shape of receptive fields influences the perception of tactile distances. As more receptive fields lie between the two equally apart tactile stimuli in the mediolateral axis (triangles) than in the proximodistal axis (squares), the perceived distance is longer in the mediolateral than in the proximodistal axis, an effect known as anisotropy. See the online article for the color version of this figure.

Surgical elongation of limbs is a highly unusual situation, which may not be representative of the effects of skin stretch on tactile processing. Given the clear effects of skin stretch on somatosensory processing, described above, we aimed to investigate how rapid changes in skin stretch influence tactile distance perception with a two-alternative force-choice paradigm. Two possible outcomes can be hypothesized: First, tactile distances might be perceived similar in size before and after skin stretch, which would imply that a top-down mechanism corrects for the amount the skin was stretched. Second, tactile distances might be perceived as smaller on the stretched skin compared to nonstretched skin, as less afferent nerve endings and therefore fewer RFs are available in the zone between the two touches due to the stretch. In this scenario, no top-down correctional mechanism would apply.

Method

In the following text, we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures used in the study.

Sample Size Calculation

To find an appropriate number of participants for the present study, we conducted a power analysis using G*Power Version 3.1.9.6 (Faul et al., 2007) to test the difference between two dependent means using a two-tailed *t* test, an alpha of .05, and an effect size ($d_z = .845$) that was derived from a comparable study investigating tactile distance perception (Longo, 2017). The analysis indicated that a minimum sample of 14 participants was required to achieve a power of .80.

Participants

In October 2019, 24 members of the Birkbeck community were recruited for this study (nine women; age $M = 35.0$, $SD \pm 12.3$ years, range = 19.6–59.2 years). Inclusion criteria were the ability to understand the experimental instructions in the English language and being over 18 years of age. Exclusion criteria, which were defined prior to execution of the study, were a history of neurological diseases and skin conditions such as eczema or scars in any of the assessment areas. Further, participants were excluded if the R^2 for the model fit of the psychometric function in either experimental condition was less than .5, consistent with other studies from our lab using this paradigm (Longo et al., 2015; Longo & Morcom, 2016). $R^2 < .5$ in one or both experimental conditions led to the exclusion of four subjects after the initial analyses. These excluded participants were replaced, bringing the final sample to 20 participants (seven women; age $M = 33.94$, $SD \pm 11.77$ years, range = 19.6–53.8 years). All but two participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; $M = 71.84$, $SD \pm 39.05$). The study was approved by the Ethics Committee of the Department of Psychological Sciences at Birkbeck, University of London and performed in accordance with the Declaration of Helsinki. All participants gave written informed consent prior to the study.

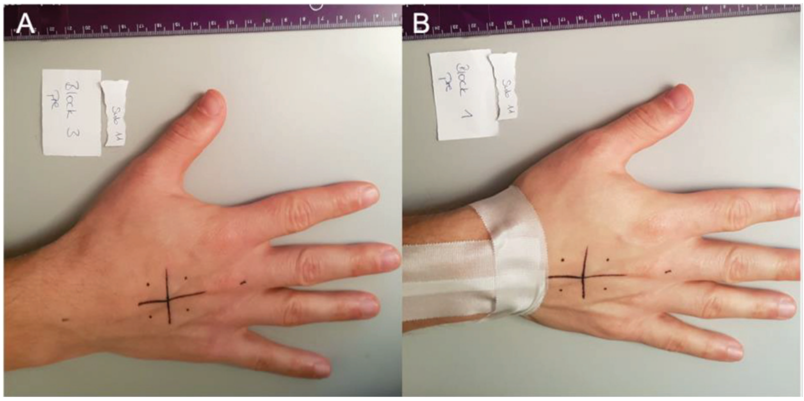
Procedure

The experimental procedure was conducted as previously described by Longo and colleagues (Longo, 2017; Longo & Haggard, 2011; Miller et al., 2014, 2016). One experimenter (Tina Mainka) conducted the task in all participants on the dorsum of the dominant hand. Participants sat in a chair during the experiment and placed their dominant hand palm-down on a table in a position that felt comfortable. Participants were blindfolded during the task. Short breaks were allowed between blocks to avoid fatigue.

The participant's hand was prepared in the following manner: On the back of the hand, a line in the proximodistal hand axis was drawn between the center of the participant's wrist and the knuckle of their middle finger. Perpendicular to this line, a second line was drawn was drawn in the mediolateral axis of the hand with the point of intersection being set approximately in the center of the dorsum of the hand. Then, four marks representing the corners of a square with a side length of approximately 2 cm were placed around the point of the intersecting lines (see Figure 2).

Participants were examined in the following two experimental conditions: the nonstretch condition without any further manipulation and the stretch condition. For the stretch condition, two strips of common surgical tape (3M Durapore, Neuss, Germany; 2.5cm width, approximately 20 cm to 25 cm long) were used to stretch the

Figure 2
Experimental Set Up



Note. Photographs of the hand were taken before and after each block. (A) Nonstretch condition. A line in the proximodistal hand axis between the center of the participant's wrist and the knuckle of their middle finger and a line in the mediolateral hand axis with the point of intersection in the center of the dorsum of the hand were drawn. Four dots representing the corners of a square with a side length of approximately 2 cm were set around the point of the intersecting lines. (B) Stretch condition. Two strips of surgical tape were applied in parallel to stretch the skin of the dorsum of the hand in the proximodistal axis from the wrist towards the elbow. Another short strip was placed in radioulnar direction above the wrist to avoid loosening of the strips inducing the proximodistal skin stretch. See the online article for the color version of this figure.

skin of the dorsum of the hand in the proximodistal axis from the wrist toward the elbow. They were applied in parallel to ensure that the skin was stretched evenly from the radial to the ulnar side of the hand. Another short strip of surgical tape (approximately 8cm) was placed in radio-ulnar direction above the wrist to avoid loosening of the strips inducing the skin stretch (see Figure 2B). The surgical tape was renewed before each block in the stretch condition.

Custom made stimuli were used consisting of pairs of wooden posts mounted in foamboard and separated by 20 mm, 30 mm, and 40mm, which is similar to those in previous studies of tactile distance perception (Calzolari et al., 2017; Fiori & Longo, 2018; Knight et al., 2014; Longo, 2017; Longo & Haggard, 2011; Miller et al., 2014, 2016). The tip of each post was an area of approximately 1mm in diameter with round edges to avoid a pricking or sharp feeling on the skin. The skin was touched simultaneously with both wooden posts for approximately 1s using a moderate level of pressure that allowed a perception of touch but was not painful. On each trial, the participant was touched twice, once in the mediolateral and once in the proximodistal axis of the hand. After each trial, participants were asked to make an unspeeded verbal two-alternative force-choice (2AFC) whether the first or the second stimulus felt bigger. As described previously, we used five different pairs of stimuli in order to create varying ratios for the distances in the mediolateral and proximodistal hand axis (20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, 40/20 mm; Longo, 2017; Longo & Haggard, 2011; Miller et al., 2014, 2016). In each trial, one of these five stimulus pairs was presented. 10 repetitions per stimulus pair were carried out per block (i.e., 50 trials per block), whereby the order of the stimuli in the mediolateral and proximodistal axis was counterbalanced within these 10 repetitions. The experiment comprised four blocks. Two blocks were conducted in the stretch condition and two blocks in the nonstretch condition. The order of blocks was counterbalanced in an ABBA fashion, with the first condition counterbalanced across participants. Within each block, trials were randomized for each participant.

Before and after each block, a photograph (2,268 pixels × 4,032 pixels) of the hand was taken from directly overhead to measure skin stretch. For size comparison, a ruler was placed beside the hand (see Figure 2). The X- and Y-pixel-coordinates of each of the 4 marks on the back of the hand and two points on the ruler 10cm apart were coded for each photograph using Preview (Version 10.1, Apple Inc., Seattle, WA).

Analysis

We used Procrustes alignment (Bookstein, 2003; Goodall, 1991; Rohlf & Slice, 1990) to superimpose the spatial configurations of the homologous corners of the square drawn on the dorsum of the hand in the nonstretch and stretch condition, respectively, by translating, scaling and rotating them to be as closely aligned to a reference shape as possible. As a first step, an ideal square was chosen as reference shape (landmarks (x, y): 0, 1; 0, 0; 1, 0; 1, 1). Second, the configurations were translated, so that their centroids (i.e., the arithmetic mean position of all points in the square) were in the same position. Third, the configurations were scaled (i.e., normalized in size) so that the centroid size (i.e., the square root of the sum of squared distances between each landmark and the centroid) was equal to 1. Forth, the configurations were rotated to receive the minimum sum of squared distances between pairs of homologous corners. In the context of the present study, we allowed mirror reflections of the configurations.

To quantify the skin stretch on the hand dorsum we found the stretch applied to the nonstretch condition that minimized the Procrustes distance with the stretch condition using a customized Matlab script. A one-sample t test was used to compare the mean minimum Procrustes distances to a ratio of 1. For this and other one-sample t test, Cohen's d was calculated as $d = M$ difference/SD. Note that the t test was carried out in log-space, but values were transformed back for reporting means. A stretch of 1 describes a square grid. Stretches >1 indicate stretch in the proximodistal hand axis, while stretches <1 indicate stretch in the mediolateral hand axis. We also used generalized Procrustes alignment to visualize the actual configurations of the square-grid on the hand dorsum in both the nonstretch and the stretch condition.

We calculated the distances between the two marks in the proximodistal and mediolateral axis using the Pythagorean theorem, respectively. Pixels were converted to cm. The distances in the proximodistal and mediolateral hand axis before and after each block were averaged. Then, Poisson's ratio, describing the effect that a material contracts in the direction perpendicular to the direction at which stretch is applied, was calculated for the skin ($\nu = -\varepsilon_{\text{mediolateral}}/\varepsilon_{\text{proximodistal}}$, whereby ε represents the strain in the mediolateral and proximodistal axis, $\varepsilon = \Delta$ length/original length).

As previously reported, the proportion of trials in which the mediolateral stimulus was judged as larger than the proximodistal stimulus was calculated for each of the five stimulus ratios (Longo, 2017). These proportions were then analyzed as a function of the stimulus ratios and plotted using a logarithmic scale on the x-axis to produce a symmetric distribution around a ratio of 1 (i.e., the ratio at which the two stimuli have the same size). Cumulative Gaussian functions were fit to the data from each participant using maximum-likelihood estimation with the Palamedes toolbox for MATLAB (Prins & Kingdom, 2018) in a customized MATLAB script. We used a lapse rate of 0, meaning that the psychometric functions used the entire range from 0 to 1.

These psychometric functions are controlled by two parameters, the mean and the slope. The Gaussian's mean indicates where it crosses .5 on the y-axis and reflects the point of subjective equality (PSE); that is, the ratio between the mediolateral and proximodistal stimuli at which they are perceived as equally large. If we assume a bias to perceive mediolateral as larger than proximodistal distances, the PSE should be smaller than 1, as the proximodistal stimulus would need to be larger than the mediolateral stimulus for them to be perceived as the same size. Conversely, for a bias to perceive proximodistal distances as larger than mediolateral distances, the PSE should be larger than 1. The slope, corresponding to $1/SD$, represents the steepness of the psychometric function, whereby the steepness positively correlates with the precision of judgements.

In order to assess anisotropy for each condition, one-sample t-tests were used to compare mean PSEs to a ratio of 1. For comparison of anisotropy between the two conditions, a paired t test was used to compare the mean PSEs. As the PSE is a ratio of two distances, these values were log-transformed before conducting the t-tests and transformed back to a ratio for reporting means. The precision of judgements represented by the slope of the psychometric function was compared between both conditions using a paired t test. For paired t tests, Cohen's d_z was calculated as $d_z = T/\sqrt{n}$.

To investigate whether the induced skin stretch correlates with the change in the PSE, we performed Pearson's correlation for the stretch parameter that minimized the Procrustes distance between the stretch and nonstretch condition (as described in the preceding text) and ΔPSE (stretch–nonstretch condition) in log-space.

To determine whether nonsignificant results provide support for the null hypothesis of no actual difference, we conducted Bayesian paired *t* tests and Bayesian correlation using JASP (JASP Team, 2022).

Results

Generalized Procrustes superposition for the spatial configurations of the homologous corners of the square drawn on the back of the hand in the nonstretch and stretch condition, respectively, is shown in Figure 3A. As expected, the minimum Procrustes distance was for stretches greater than 1, indicating significant skin stretch in the proximodistal direction (mean stretch parameter = 1.20), $t(19) = 10.77$, $p < .0001$, $d = 2.41$ (see Figure 3B). Of note, the Poisson's ratio for the skin was .39 ± .29.

Experimental results on a group level are shown in Figure 4. Individual participant data is plotted in Figure 5 and Figure 1 in the online supplemental material.

The R^2 values indicated good fit of the data to the Gaussian functions in both conditions (nonstretch, $M = .97$, $SD \pm .04$; stretch, $M = .95$, $SD \pm .07$). Clear anisotropy was seen for both the nonstretch, mean PSE .88, $t(19) = -4.51$, $p < .0001$; Cohen's $d = 1.01$, and the stretch condition, mean PSE .69, $t(19) = -9.26$, $p < .0001$; Cohen's $d = 2.07$. Importantly, the magnitude of anisotropy differed significantly between the nonstretch and the stretch condition, $t(19) = 6.13$, $p < .0001$, $dz = 1.37$. Notably, the PSE was smaller in the stretch than in the nonstretch condition in each of the 20 participants (see Figure 5, left panel). The slope of the psychometric function and therefore the precision of judgements did not significantly differ between conditions, $t(19) = 1.56$, $p = .14$, $d_z = .35$; see Figure 5, right panel). Bayes factor (BF) offered anecdotal evidence for the null hypothesis in favor over the alternative hypothesis ($BF_{01} = 1.519$).

The amount of skin stretch represented by the stretch parameter that minimized the Procrustes distance between the stretch vs. non-stretch condition did not correlate significantly with the change in the PSE between stretch and non-stretch condition ($r = 0.22$, $p = 0.34$). Bayesian correlation provided anecdotal evidence for the null hypothesis compared to the alternative hypothesis ($BF_{01} = 2.37$).

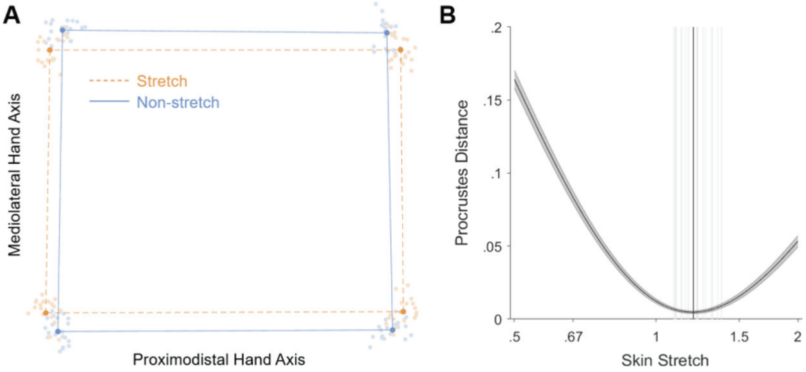
Discussion

We explored the influence of skin stretch on tactile distance perception with a two-alternative forced-choice paradigm on the back of the hand in a sample of healthy participants. As shown previously, there was an anisotropy of tactile distance perception with tactile distances being perceived as smaller in the proximodistal axis (Fiori & Longo, 2018; Knight et al., 2014; Longo et al., 2015; Longo & Haggard, 2011; Mainka et al., 2021). This anisotropy was significantly pronounced after stretch of the skin along the proximodistal direction. We therefore for the first time showed, that skin stretch on the back of the hand leads to a perception of tactile distances as smaller as on skin without applied strain.

The evaluation of distances between two tactile stimuli on the skin is most likely a basic somatosensory feature that is computed at a low cortical level of somatosensory processing (Calzolari

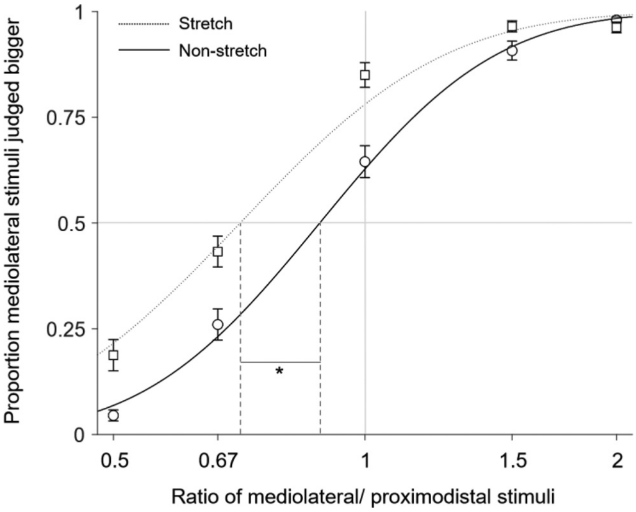
Figure 3

Analysis of Experimental Skin Stretch



Note. (A) Generalized Procrustes superposition of the actual configuration of the square-grid on the hand dorsum in both the nonstretch (blue dots, solid lines) and the stretch (orange dots, dashed lines) condition. The dark dots represent the averaged shape, whereas the light dots are individual participant's data. (B) Mean Procrustes distance between the grid on the back of the hand in the nonstretch and stretch condition which was mathematically stretched in the proximodistal axis by various amounts. The shaded region indicates one standard error of the mean. A stretch of 1 indicates no skin stretch, whereas stretches >1 indicate a stretch in the proximodistal hand axis. The light gray vertical lines indicate the stretch that minimized the Procrustes distance between the grid in the nonstretch and the stretch condition for each individual participant, while the black vertical line is the average for all participants. As we experimentally stretched the skin in the proximodistal direction, each participant had a stretch >1. See the online article for the color version of this figure.

Figure 4
Experimental Results



Note. Data from the curves fit to data are cumulative Gaussian functions. The dashed vertical lines highlight the points of subjective equality (PSE) for both conditions (i.e., the point at which the curve crosses 0.5). For both conditions, the PSEs were smaller than 1, indicating clear anisotropy (i.e., the distances in the mediolateral hand axis were perceived as larger than in the proximodistal axis). The magnitude of anisotropy was greater in the stretch condition (*$p < .0001$). Error bars indicate one standard error.

et al., 2017). In fact, a study combining a behavioral paradigm and functional MRI has recently shown that the internal geometry of tactile space could be reconstructed from neural data (Tamè et al., 2021). The distorted organization of tactile space with the mediolateral limb axis being overrepresented compared to the proximodistal limb axis, which can similarly be found in the receptive field (RF) geometry in the dorsal horn of the spinal cord (Brown et al., 1975), is also preserved in the contralateral primary sensorimotor cortices (Tamè et al., 2021). As oval RFs in the somatosensory cortex are four to five times longer than broad (Brooks et al., 1961), a much larger anisotropy than found in typical behavioral experiments with stimuli in the mediolateral axis being approximately 40% larger than in the proximodistal axis would be expected (Longo & Golubova, 2017; Longo & Haggard, 2011). Therefore, an additional correctional process needs to be implemented to reduce the distortions in tactile size perception between different body axes (Tamè et al., 2021).

Correctional processes influencing size estimation therefore already exist in our central nervous system. In case such a top-down mechanism would also correct for skin stretch, tactile distances would have been perceived similar in size before and after skin stretch, which our data do not support. In contrast, we found that tactile distances were estimated as smaller on the stretched skin compared to nonstretched skin, similarly to the result that Anstis and Tassinary (1983) received when they investigated tactile size estimation on broadly smiling and crimped lips. Together with the afore mentioned case of an achondroplastic patient who underwent elongation surgery of her upper extremities and, after surgery, clearly underestimated tactile distances on the arms with by then stretched skin (Cimmino et al., 2013) there are now several pieces of evidence supporting the assumption that the central nervous system does *not* take skin stretch into account when calculating distances between two tactile stimuli.

This is rather surprising, as sensitivity to skin stretch has already been demonstrated by direct recordings from peripheral afferent fibers for the first time over half a century ago in cats (Burgess et al., 1968; Chambers et al., 1972), monkeys (Kumazawa & Perl, 1977; Perl, 1968), rabbits (Appenteng et al., 1982; Shea & Perl, 1985), and rats (Grigg, 1996). However, the corresponding end organ, its mechanism and ultimate role in somatosensation is still poorly characterized (Handler & Ginty, 2021). In humans, sensitivity of afferent fibers to skin stretch has been demonstrated for the glabrous skin of the palm (Hulliger et al., 1979; Knibestöl & Vallbo, 1970), as well as for the hairy skin of the dorsum of the hand (Edin, 1992, 2004; Edin & Abbs, 1991; Grill & Hallett, 1995) and the knee (Edin, 2001).

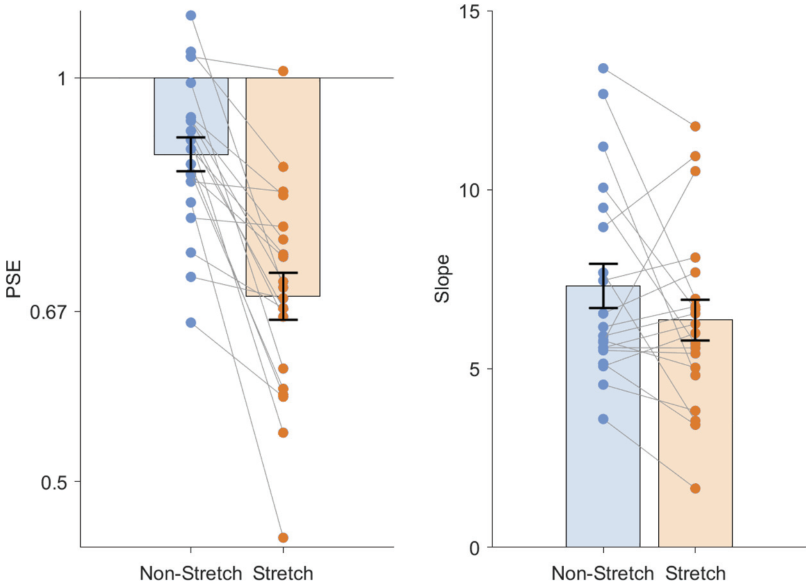
Within our body, skin stretch occurs mostly through movement of joints in the adjacent tissue. Indeed, the activation of peripheral afferents by skin stretch also elicits responses in the central nervous system, as demonstrated by a study that recorded tactile activity in the somatosensory cortex of primates during arm movements while avoiding other tactile input (Cohen et al., 1994). Therefore, tactile signals of skin stretch might contribute to position sense (Edin & Abbs, 1991; Moberg, 1983). This is also supported by several other findings: For instance, skin stretch of the hand dorsum evoked the illusion of finger movement (Collins & Prochazka, 1996), which was also shown for the elbow and knee (Collins et al., 2005). Similarly, movement illusion could be induced by electrical stimulation of cutaneous SA type II afferents of the hand (Macefield et al., 1990). Moreover, perceived finger joint positions could be derived from skin strain patterns (Edin & Johansson, 1995).

We examined the skin on the back of the hand between the wrist and metacarpophalangeal joints, and therefore a strip of skin that is subject to physiological stretch when the adjacent joints are moved. We can only speculate how results would have been on parts of skin that undergo even more physiological stretch (e.g., the skin directly over a joint, such as the wrist) or spots of skin that usually are not stretched (e.g., the skin in the middle of the forearm or thigh). It is also unclear, whether skin stretch in other directions would lead to similar results. However, as we were able to show that skin stretch leads to the perception of distances as shorter in *every* of our 20 participants, we can assume that this is a robust finding that would be reproducible in broader age groups in populations without diseases of the peripheral and central nervous system as well.

One explanation for our result might be hypothesized as follows: In the two-dimensional grid of tactile space, estimation of tactile distances is presumably facilitated by "counting" the RFs between the stimulated locations (Longo & Haggard, 2011). When skin is stretched, less afferent nerve endings and therefore fewer corresponding RFs are available within the same external reference frame. Oversimplifying, we could assume that a 2-cm strip of skin on the back of the hand covers 20 RFs (i.e., 1 RF/mm skin). If the skin is stretched by 20%, the same 20 RFs now cover 2.4cm of stretched skin (i.e., 1 RF/1.2mm). On the nonstretched skin, tactile stimuli with 2-cm distance would therefore be 20 RFs apart, whereas on stretched skin, the same 2-cm distance would roughly

Figure 5

Mean and Individual Points of Subjective Equality and Slopes



Note. Left panel. Bars show the mean point of subjective equality (PSE; i.e., the ratio of mediolateral/proximodistal stimuli that was perceived as equally large) across participants, error bars show the standard error for the nonstretch (blue) and stretch condition (orange). Circles indicate the individual participant's PSE with gray lines connecting the same participant's data for the nonstretch and stretch condition. Note that the PSE is smaller in the stretch condition for each participant. Right panel. Bars show the mean slope (i.e., the steepness of the psychometric function) across participants, error bars show the standard error. Circles indicate the individual participant's slope with gray lines connecting the same participant's data for the nonstretch and stretch condition. See the online article for the color version of this figure.

only be 17 RFs apart. Thus, according to the pixel-model, skin stretch leads to the perception of tactile distances as shorter.

Accordingly, this "elimination" of available RFs in the proximodistal axis of the hand by stretching the skin in the same direction as applied in our experiment led to an increase in tactile distance anisotropy. In theory, more skin stretch would lead to an increased "elimination" of available RFs and therefore to the perception of tactile distances as even shorter. Interestingly, however, we found no such correlation between the amount of skin stretch and the change in the point of subjective equality between both conditions. First, this result might simply be due to a lack of power to answer this secondary objective. Second, however, this might be owed to the experimental set-up we employed here: With our two-alternative forced-choice paradigm, the distinction whether the proximodistal or mediolateral stimulus felt larger was collected for five different stimulus ratios. This is the most robust design to show anisotropy in tactile distance perception, which was our primary goal here, but does not allow to collect continuous data on how large a stimulus felt in proper units of distance measurement. Therefore, the hypothesis that the amount of skin stretch correlates with the actual change in tactile distance estimation should be investigated with a paradigm that collects data on distances between stimuli on a continuous scale (e.g., Fiori & Longo, 2018; Mainka et al., 2021). Third, the lack of correlation might be explained by the limited amount of RFs in a defined skin area. Once the skin is stretched so far, that even further skin stretch would not result in a lesser amount of available RFs, there would be no variance in tactile distance perception anymore and therefore no mathematical prerequisite for a meaningful correlation would be given.

Well over 70 years ago, Halpern first described a condition he coined "dermatokinesthesis" (Halpern, 1946). He reported patients in whom spinal or cerebral lesions led to an impairment to perceive the direction in which skin is (passively) moved and remarked, that this loss of function is always accompanied by a deficit of sense of position in the same body part, but not a disturbance to detect touch (Halpern, 1949). Similarly, in an interventional study using digital nerve blocks, it has been shown that the perception of finger position depends highly on afferent input from the skin and not from muscle spindles alone (Ferrell & Milne, 1989).

Unfortunately, this knowledge has in a way been neglected in the past—not only clinically, but also for trying to study somatosensation, the effect of mechanical skin strain on statesthesia and kinesthesia and their influence on the pathophysiology of certain diseases. Indeed, physical manipulation of the skin might influence the examination of tactile distance discrimination which seems to be of major importance for the investigation of body parts close to joints (e.g., the hand and fingers) or body parts in which the skin is particularly mobile (e.g., the back). This implies that physical strain to the skin through factors such as scars, burns or kinesiotaping—

even if not directly in the testing area—might bias the results similarly to different postures of body parts while testing. One disease for which this might be of particular interest is dystonia, a movement disorder characterized by sustained or intermittent muscle contractions that cause abnormal and often repetitive movements and/or postures, either confined to a certain body part such as the hand ("focal hand dystonia," "writer's cramp") or neck ("cervical dystonia") or affecting larger portions or even the whole body ("generalized dystonia"; Albanese et al., 2013). Some earlier studies indeed have shown impaired spatial discrimination in several forms of isolated focal dystonias (for review, see Conte et al., 2019) which could not be confirmed in a recent study using a behavioral paradigm that reflects central organization of tactile space (Mainka et al., 2021; Tamè et al., 2021). Interestingly, impaired proprioception has also been discussed as a pathophysiological feature in dystonia (Conte et al., 2019), whereby it is still under debate, whether disturbed proprioception can be regarded as a predisposition or a cause of the disease (Conte et al., 2019). It also would be highly interesting to study the previously neglected, but through abnormal postures permanently existing component of skin stretch to the perception of self-position and self-movement in dystonia.

Regarding other physiological functions of skin stretch, it could be hypothesized that the central responses to skin stretch might also contribute to our body model that contains information about our body's metric properties (Longo & Haggard, 2010). Here, information about skin stretch might help to code (volu)metric measures of body parts that do not have a constant size, such as a foot or an arm, but rather fluctuate in their appearance as the abdomen before and after a proper meal or during pregnancy.

In conclusion, our study showed that tactile distances are perceived as shorter when the skin is stretched in the direction of the stimulus orientation. We assume that this effect is owed to the 'removal' of afferent nerve endings and corresponding RFs by skin stretch that are no longer available within the same external reference frame for size estimation between the two applied tactile stimuli. Though represented centrally, the skin stretch does not seem to trigger the use of a correction factor to account for the bias in tactile distance estimation. We have also highlighted the previously neglected important aspect of skin stretch to the perception of self-position and self-movement and discussed its possible neurobiological roles in health and disease.

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