The relation between human hair follicle density and touch perception

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Unmyelinated low threshold C-tactile fibers moderate pleasant aspects of touch. These fibers respond optimally to stroking stimulation of the skin with slow velocities (1–10 cm/s). Low threshold mechanoreceptors are arranged around hair follicles in rodent skin. If valid also in humans, hair follicle density (HFD) may relate to the perceived pleasantness of stroking tactile stimulation. We conducted two studies that examined the relation between HFD and affective touch perception in humans. In total, 138 healthy volunteers were stroked on the forearm and rated the pleasantness and intensity. Stimulation was performed by a robotic tactile stimulator delivering C-tactile optimal (1, 3, 10 cm/s) and non-optimal (0.1, 0.3, 30 cm/s) stroking velocities. Additionally, a measure of discriminative touch was applied in study 2. HFD of the same forearm was determined using the Cyanoacrylate Skin Stripping Method (CSSM), which we validated in a pretest. Women had higher HFD than men, which was explained by body size and weight. Furthermore, women rated affective touch stimuli as more pleasant and had higher tactile acuity. Depilation did not affect touch perception. A weak relationship was found between the C-tactile specific aspects of affective touch perception and HFD, and the hypothesis of HFD relating to pleasant aspects of stroking only received weak support.

The hair follicle is surrounded and innervated by a large network of sensory afferents1 and it has long been suggested that hair follicles are important for the sense of touch3. The aim of the current studies was to test whether hair follicle density (HFD) is related to the affective component of touch.

Hair follicles are present all over the body, except for the palms of the hands, the soles of the feet, the genitalia and the lip vermilion3–6. The adult human has three types of hair: terminal, vellus and intermediate hair. The terminal hairs are thick and pigmented and can be found in androgen-dependent areas (e.g. scalp, beard and axilla) and in some androgen-independent areas (such as the eyebrows). Vellus hairs are thin, short and unpigmented and cover the whole body, except for the glabrous skin. Intermediate hairs can be described as a mixture between the terminal and vellus hairs and are found together with the vellus hairs on the arms and legs of adults1. All hair follicles are developed early in the fetal period and no new hair follicles are formed after birth, implying that HFD in an adult will depend on how much that particular body part grows after the formation of the hair follicles7. This has two interesting consequences: First, it can be assumed that there is a certain inter-individual variation of HFD and this variation will be rather stable over time, with some degeneration being possible. Hence, a person with low HFD will remain a person with low HFD. Second, HFD in the adult depends on the degree of growth of particular body parts after the formation of the hair follicles7. Correspondingly, the density of hair follicles is highly variable over the human body, with highest densities in the face and lowest in the more distal parts of the body, such as the calf8–9.

Recent work in mouse hairy skin has shown that the hair follicles are innervated by C low threshold mechanoreceptors (C-LTMRs)10,11. The terminal projections of C-LTMRs are only found in hairy skin and they appear to encircle and penetrate the hair follicle11. Furthermore, C-LTMRs selectively innervate certain types of hair follicle,
namely the awl/auchene and zigzag, but not guard hair follicles\textsuperscript{18}. Furthermore, the dorsal root ganglia (DRGs) innervating distal limbs contain fewer C-LTMRs than DRGs innervating proximal limbs\textsuperscript{10}.

The human equivalent to the C-LTMRs are called C-tactile afferents. The C-tactile afferents, which exist exclusively in hairy skin, respond optimally to a slow, light stroking (1–10 cm/s) delivered at skin temperature. Stroking the skin at faster and slower velocities decreases the firing frequency. The characteristics of C-tactile optimal stroking correspond to a human-to-human care\textsuperscript{12–15} and the firing frequency is correlated with subjective ratings of perceived pleasantness\textsuperscript{13}. C-tactile afferents have also been suggested to be involved in detecting the erotic component of touch to non-genitalia skin\textsuperscript{3,14}. Taken together, the main role of these nerve fibers appears to be the moderation of the affective experience of touch\textsuperscript{15}. It has been further shown that adults who are asked to apply a stroking caress to their infant or their partner, spontaneously use velocities that target C-tactile afferents\textsuperscript{17}.

The density of C-tactile afferents appears to predict the perceived pleasantness of tactile stroking stimulation. In a group of rare patients suffering from a significant reduction of thin nerve fibers, including C-tactile fibers, ratings of perceived pleasantness were significantly reduced compared to healthy controls\textsuperscript{18}. Other clinical disorders where altered C-tactile processing has been found include for example autism\textsuperscript{19,20} and anorexia nervosa\textsuperscript{21}.

The discriminative properties of touch on the other hand, such as object identification, are mainly processed by thick, fast conducting, myelinated A\textsuperscript{β} afferents\textsuperscript{22}. In contrast to C-tactile fibers, the firing frequency of A\textsuperscript{β} afferents increases linearly with increasing velocity\textsuperscript{13}. The firing frequency of A\textsuperscript{β} afferents is correlated with ratings of touch intensity\textsuperscript{19}.

One way to present the C-tactile specific experience of touch is by measuring pleasant touch awareness. This variable represents the C-tactile specific, mainly peripherally moderated experience of touch. It has been shown before, that pleasantness ratings to stroking stimulation show a strong correlation to the firing frequency of C-tactile fibers and that the C-tactile firing frequency follows an inverted U-shaped curve\textsuperscript{13}. We therefore assume, that a high bending of the curve reflects the perception of C-tactile mediated aspects of touch. This bending is calculated as the rating difference of C-tactile optimal vs. sub-optimal stroking velocities, weighted by the overall touch ratings\textsuperscript{19}. The overall touch pleasantness on the other hand represents a top down modulated experience of touch and is calculated as averaged ratings over all stroking velocities\textsuperscript{19}. The stimulation of A\textsuperscript{β} afferents in a stroking experiment is best captured by ratings of intensity\textsuperscript{19}. Another measurement of A\textsuperscript{β} signaling is the two-point discrimination threshold.

We hypothesized, that human hair follicles could be associated with C-tactile afferents in a similar way as shown in mice. Affective touch perception may depend on C-tactile fiber density and positively relate to HFD. The spatial summation of C-tactile input to the central nervous system due to higher HFD and C-tactile fiber density may thus be encoded as higher levels of pleasant touch awareness.

To examine the relationship between HFD and affective touch perception, we first defined the forearm as a body site representative for the overall HFD of the body using the cyanocrylate skin stripping method (CSSM)\textsuperscript{7}. Secondly, in a small subsample we tested whether depletion changed the perception of touch stimulation. These two pretests are presented in the methods section. We then tested HFD and the affective perception of slow C-tactile afferent targeting stroking, in order to determine a potential correlation. Using a robotic device validated for psychophysical examination of hedonic qualities of touch\textsuperscript{23}, participants were stroked with C-tactile optimal (1, 3, 10 cm/s) as well as non-optimal (0.1, 0.3, 30 cm/s) velocities (compare previous studies\textsuperscript{15,24,25}) and asked to rate the affective domains of pleasantness and eroticism. The relation between C-tactile afferent stimulation and non-genitalia directed erotic touch perception has been shown in a recent paper\textsuperscript{16}. The ratings of eroticism are presented in the supplementary information.

According to previous work\textsuperscript{19}, two main affective touch outcome variables were defined: The pleasant touch awareness and the overall touch pleasantness. In an additional study, we replicated and extended study 1. Ratings of intensity and two-point discrimination (study 2) were included in order to test for discriminative, A\textsuperscript{β} mediated, touch. We also assessed gender differences in HFD, discriminative and affective touch perception.

**Results**

**Moderators of hair follicle density.** In the first study, the HFD of the forearm skin was successfully calculated in 55 out of 58 participants samples, yielding a mean number of 37.4 ± 10.0 hair follicles per cm\textsuperscript{2} (range: 17–59). HFD was significantly negatively correlated to the weight of the participants (r = −0.303, p = 0.031) and further negatively related to the body height, however this correlation was not significant (r = −0.247, p = 0.1). Hence, the height and weight were included as covariates in the following analysis of gender differences.

Although women displayed a higher HFD than men (women: N = 33, mean 38.39 ± 9.52; men: N = 22, mean 35.91 ± 10.77, compare Fig. 1), the difference was not significant after inclusion of weight and height in the analysis (F[51] = 0.36, p = 0.6).

The results of HFD calculations in study 1 were replicated in study 2. Here, HFD was successfully calculated in all 80 samples, displaying a mean number of hair follicles per cm\textsuperscript{2} of 40.38 ± 13.29 SD (range: 17–84) and HFD decreased with increasing volume of the participant’s body (correlation to height: r = −0.312, p = 0.005; to weight: r = −0.164, p = 0.2). There was a significant difference in HFD between men and women with women displaying a higher number of hair follicles per cm\textsuperscript{2} compared to men (women: 43.37 ± 14.23/cm\textsuperscript{2}; men: 35.1 ± 9.58/cm\textsuperscript{2}). However, this difference was not significant after inclusion of weight and height as covariates in the analysis (F [79] = 1.3, p = 0.3; Fig. 1).

**Combined analysis.** The datasets of the original and the replication study were combined in order to allow detection of subtle effects by an increased sample size of 135 participants in total. This was possible, as the participants of both studies did not differ significantly in gender distribution (p = 0.6), age (p = 0.1), weight (p = 0.8), height (p = 0.7), BMI (p = 0.3) or HFD (p = 0.2).
Over all participants, the HFD was significantly correlated to participants' weight ($r = -0.203$, $p = 0.021$) and height ($r = -0.286$, $p = 0.001$). Again, women had a higher HFD (mean $41.4 \pm 12.8$ SD) than men (mean $35.5 \pm 10$ SD, compare Fig. 1) and again those differences were not significant after inclusion of weight and height as covariates ($F[1, 129] = 0.43$, $p = 0.5$).

**Perception of affective and discriminative touch.** For analysis of the perception of affective and discriminative touch, different measurements can be distinguished: the general perception of affective touch is measured by the overall touch pleasantness, whereas C-tactile mediated affective touch perception is described by pleasant touch awareness (for calculation of these values, see Methods section). The discriminative touch perception mediated mainly by Aβ fibers was determined through the overall intensity ratings and, in study 2, the two-point discrimination threshold.

In the first study, pleasantness ratings of different stroking velocities followed an inverted U-shape peaking at 3 cm/s (main effect of velocity: $F[2.7, 153.9] = 15.8$, $p < 0.001$; compare Fig. 2). Further, there was a significant main effect of velocity on intensity ratings ($F [2.3, 129.4] = 10.0$, $p < 0.001$), where faster velocities were rated as more intense than slower velocities.

The overall touch pleasantness differed between male and female participants with women rating pleasantness higher than men ($F[1, 55] = 4.7$, $p = 0.034$). There was no significant interaction effect between gender and velocity (pleasantness: $p = 0.5$) and no significant gender difference on pleasant touch.

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**Figure 1.** Hair follicle density of the forearm compared between men and women in study 1, study 2, and the combined sample. There was no significant difference in HFD between men and women in study 1. Women presented higher HFD on the forearm in study 2 and in the combined sample. However, this difference was explained by women's smaller body size. On the x-axis the density of the HFD is plotted. The black line represents the statistical mean value, the red and blue lines, respectively, represent 95% confidence intervals.

**Figure 2.** Gender-specific pleasant touch perception. Ratings of perceived pleasantness compared between men and women in study 1 and study 2. Female participants rated higher across all applied stroking velocities than male participants. The error bars represent 95% confidence intervals.
Combined analysis. Comparison between the studies revealed a significant difference in the overall touch pleasantness (t [134] = 3.05, p = 0.003) with ratings being higher in the sample of study 2. Ratings for pleasant touch awareness and for overall touch intensity did not differ between the sample groups (pleasant touch awareness: p = 0.72; overall touch intensity: p = 0.64).

Over all participants, the significant effect of gender on touch perception remained stable, with women rating pleasantness and the intensity of touch higher than men (pleasantness: F[1, 135] = 15.0, p < 0.001, intensity: F[1, 135] = 16.0, p < 0.001). Furthermore, overall touch pleasantness and overall touch intensity differed significantly between men and women (p < 0.001, compare Fig. 3 for overall touch pleasantness). There was no interaction effect between gender and velocity on the ratings (pleasantness: p = 0.4). In line, there were no significant gender differences in pleasant touch awareness (p = 0.8), indicating that the shape of the inverted U curve did not differ between the genders.

Perception of touch in relation to HFD. In study 1, there was no significant correlation between HFD and pleasant touch perception (overall touch pleasantness: r = 0.079, p = 0.6; pleasant touch awareness: r = 0.028, p = 0.8). Furthermore, there was no correlation between intensity ratings and HFD (overall touch intensity: r = 0.180, p = 0.2). Inclusion of height and weight as control variables resulted in no changes of the correlations.

The result from study 1 was mainly replicated in study 2. Again, HFD was not related to overall pleasantness (r = −0.112, p = 0.322) or overall touch intensity (r = 0.039, p = 0.746) and there was no significant correlation between HFD and the two-point discrimination threshold (r = 0.027, p = 0.8). However, HFD correlated positively to pleasant touch awareness (r = 0.269, p = 0.016, compare Fig. 4), implying that a high pleasantness rating to C-tactile specific stimulation was related to higher HFD. Inclusion of weight and height as control variables did not change the results: the correlation between HFD and pleasant touch awareness remained stable (r = 0.261, p = 0.024), all other correlations were non-significant.

Combined analysis. Combining the data from both studies revealed no significant correlations between the HFD and measures of touch (overall touch pleasantness: r = −0.012, p = 0.9; pleasant touch awareness: r = 0.134,

**Figure 3.** Two-point discrimination (study 2) and overall touch pleasantness (combined sample). Women present a lower two-point discrimination threshold than men. Touch pleasantness ratings were higher for women than men in the pooled data set (study 1 and 2). In the representation of overall touch pleasantness, the density is plotted on the x-axis. The black line represents the statistical mean value, the red and blue lines, respectively, represent 95% confidence intervals. The numbers and color codes on the bar representing the female values describe the distance of the two indenting stimuli in the course of the assessment.
p = 0.1; overall touch intensity: r = 0.096, p = 0.3). Inclusion of height and weight as control variables did not change the results.

Discussion

The aim of the present studies was to investigate a potential relationship between HFD on the human forearm and affective touch perception from stimulation to the same body site. However, a relation between HFD and affective touch perception was only found for study 2, where pleasant touch awareness was moderately correlated with HFD. Interestingly, this result was neither found in study 1, nor in the overall sample. Previous studies have found C-LTMRs to be distributed around hair follicles10, 11, leading to our hypothesis that C-tactile afferents are associated to hair follicles in a similar way in humans and that this influences the perception of stroking touch stimulation. We only found weak support for this hypothesis. Several aspects should be considered here: Li and colleagues used genetic labeling to visualize the distribution of nerve fibers in rodent skin. In comparison, our approach was less specific and relied on the assumption that differences in C-tactile fiber density are reflected in affective touch perception. Although it has been shown that pleasant touch perception relates to C fiber density18, it is not clear, how C fiber density impacts affective touch perception specifically. We assumed this relation to be linear with a higher density of C-tactile fibers resulting in higher ratings of perceived pleasantness, but a staircase model is likewise conceivable. Hence, the C-tactile density may not be important for affective touch perception as long as a critical amount of intact C-tactile fibers are present. In our sample of healthy people, it is very likely that such a critical amount would be conserved in all participants. On the other hand, disturbances in affective touch perception have been found in patients suffering from anorexia nervosa21. These patients have a very low body volume and, following the argument that all hair follicles are formed in utero, should have more densely packed hair follicles and thereby also higher density of C-tactile afferents. However, in these patients the potentially higher density of C-tactile afferents does not increase the pleasantness ratings. On the contrary, the ratings are decreased compared to normal participants21.

Our hair follicle density measurement was based on skin sample counting. Although we made every effort to ensure reliability of this method and our findings are in very good alignment with previous results1, some questions remain unanswered. For instance the hair shaft length and even type of hair growing in the follicle can vary with the hair follicle cycle and is influenced by internal and external factors such as hormonal levels or lifestyle26, 27. This may impact the visibility of the hair follicles under the microscope. Another limitation of the study is the conduction of the experiment on one body site only, the forearm. However, this site is representative for pleasant touch perception28 and seemingly represented the individual HFD well.

Taken together, HFD in healthy subjects does not strongly relate to human affective touch perception and, as far as we tested this, it neither relates to human discriminative touch perception. However, the study revealed more interesting results, which are worth further discussion.

The presented results describe the determination of the forearm as a body site representing the overall hair follicle density of the body and reproduce findings on the distribution of hair follicles across the body2. To the best of our knowledge, gender differences in HFD have not been reported before. Women are typically smaller than men29, which is confirmed in our sample. Differences in body size should matter for HFD as hair follicles are formed in utero30 and the HFD in the adult is dependent on the growth of the different body parts. Indeed, we found a negative correlation between HFD and weight of the participants in study 1 as well as a negative correlation between HFD and height in study 2. Over the whole sample, both height and weight significantly related to HFD. The higher HFD in women was thus fully explained by gender differences in body size.

For affective touch perception, our results confirmed the previously reported inverted U-shape of the ratings for pleasantness (e.g. refs 12, 16, 22 and 24). The differences of the rating levels between study one and two are

![Figure 4. Affective touch perception in relation to HFD in study 2. There was a positive correlation between pleasant touch awareness and HFD in study 2 across all participants. The dotted lines represent the two regression lines obtained by regressing pleasant touch awareness on hair follicle density and vice versa. The depicted r represents the Pearson correlation coefficient.]
most likely explained by slight methodological differences (anchors of visual analogue scales and application of an additional velocity in study 2).

Women rated the stroking stimulation as more pleasant, irrespective of whether touch was applied at C-tactile optimal or suboptimal velocities. This effect has been observed in previous work. Further, women rated all stroking stimulations as more intense and had a lower two-point discrimination threshold. This suggests that women are more sensitive to affective and discriminative aspects of touch, however no consistent gender differences were found for the shape of the curve (measured as pleasant touch awareness) which describes C-tactile specific perception.

The gender differences could potentially be explained by differences in peripheral nerve density, top-down processing or a combination of the two. It is worth noting that affective touch on the peripheral level is mediated by input of both C-tactile and Aβ afferents. The lack of a difference in pleasant touch awareness suggests that the proportion of peripheral C-tactile input is similar for both sexes. The differences in discriminative sensitivity suggest a higher density of Aβ afferents in women. Obviously, this is an oversimplification since spinal cord and brain processing play a substantial role for the tactile experience. A similar gender effect on discriminative touch perception on the fingertips was previously reported and related to the size of the fingertips. The potentially higher afferent input in women may explain the gender specific affective touch rating differences: such a higher input may not only increase the perceived intensity of stroking but also the pleasantness by making the tactile stimulation more perceivable. In addition, top-down influences may mediate the gender effects of affective touch perception. In general, top-down processing has been shown to have a modulatory effect on the perception of touch. Potential factors of bias, such as effects of expectancy, effects of the investigator or interpretation of the scales might differ between genders and thereby affect touch perception. All data collection was done by female researchers which potentially influenced the rating behavior of men and women differently, something that has been seen in rating behavior of pain previously. For the ratings, individuals could have had different concepts of what the terms pleasant or intense entail; potentially this could be gender specific and to some degree explain the differences in ratings.

Conclusion
Extrapolating from the findings by Li et al. where C-tactile fibers were found to be located around specific types of hair follicles in mice, we formed the hypothesis that the number of hair follicles would indicate the underlying C-tactile afferent density in human hairy skin and this would in turn affect the perception of affective touch. Only weak support for this hypothesis was found. However, important findings of gender differences in ratings of touch perception were made. These factors should be considered in future studies exploring affective touch in humans.

Methods
Participants. Fifty-eight participants took part in study 1 (34 female; mean age 26.2 years ± 6.3 years SD, range 19–51 years; for more demographic data compare Table 1). Most of these participants (N = 47) were also included in a previous study. Exclusion criteria were subjectively good health, good knowledge of the Swedish language and age above 18 years. Exclusion criteria were any skin condition, impairments of the sense of touch or sight, and allergic reaction to cyanoacrylate. 11 of the participants also participated in a small study on the effect of hair on the perception of touch.

Eighty participants took part in the replication study - study 2 (51 female, mean age 24.86 ± 4.1 years SD, range 18–36 years; for more demographic data compare Table 1). Exclusion criteria were subjectively good health, good knowledge of the German language and age between 18 and 40 years. Exclusion criteria were any skin condition, impairments of the sense of touch or sight, and allergic reaction to cyanoacrylate.

All participants received financial reimbursement for their participation. Ethical approval was obtained from the central ethics committee of the University of Gothenburg in Gothenburg, Sweden (study 1) as well as the ethics committee of Dresden University of Technology (study 2), respectively. The studies were performed according to the Declaration of Helsinki on Biomedical Research Involving Human Subjects. All participants received information about the study prior to signing informed consent.

Tactile stimulation and psychophysical ratings. For study 1, the participants were seated in a comfortable chair in front of a computer screen. Stroking tactile stimulation was applied to the left (N = 47) or to the right dorsal forearm (N = 11). The stimuli were delivered by a soft brush (6 cm wide paintbrush made of soft goat’s hair) attached to a robotic device (Rotary Tactile Stimulator, RTS, Dancer design; St Helens, UK). Stimuli were applied over a distance of 6.5 cm with a force of 0.4 N using five different stroking velocities: 0.3, 1, 3, 10 and 30 cm/s. The intermediate velocities (1, 3 and 10 cm/s) activate C-tactile afferents optimally while faster and slower velocities 0.3 and 30 cm/s activate C-tactile afferents sub-optimally. Each velocity was repeated three times in a pseudorandomized order, such that no two subsequent stimulations were of the same velocity. To remove environmental disturbances, the participants wore headphones playing pink noise at a comfortable volume. They also wore visually shielding goggles to prevent them from seeing the stimulation.

After each brush stroke the participant was asked to rate the stimulus on visual analog scales (VAS) that appeared on the computer screen. For each stimulus three properties were rated: pleasantness (anchors: extremely unpleasant (−10) and extremely pleasant (10)), intensity (anchors: not at all intense (0) and extremely intense (20)) and eroticism (see supplementary data). The participant indicated his/her VAS rating using a computer mouse positioned within easy reach on the non-stimulated side. The ratings were automatically translated into numerical values. The participants were ensured that the rating procedure would not be supervised.

In study 2, the participants first received the same tactile stimulation on the left forearm as described above for study 1, with the exception that six velocities (0.1, 0.3, 1, 3, 10 and 30 cm/s) were administered instead of five. As
The effect of hair on the perception of touch. In a second pre-test, the effect of the hair on the perception of touch was assessed. The hair on the left forearm was chemically removed using hair removal crème (Veet; Reckitt Benckiser, UK) in eleven participants (7 female, mean age = 25.182 ± 3.710 SD, range 19–30 years). Those
Table 2. Hair follicle densities at the 9 sampled body sites in pretest (N = 15), their correlation with the overall mean density and with each other.

| Body site | Mean ± SD | Correlations (significant results printed bold) |
|-----------|-----------|-----------------------------------------------|
| Forehead  | 285.0 ± 84.1 | r = 0.465, p = 0.08 r = 0.286, p = 0.172 r = 0.382, p = 0.160 r = 0.244, p = 0.340 r = 0.053, p = 0.853 r = 0.035, p = 0.901 |
| Neck      | 47.3 ± 17.1  | r = 0.130, p = 0.643 r = −0.083, p = 0.769 |
| Chest     | 28.4 ± 6.4   | r = 0.667, p = 0.007 r = 0.289, p = 0.296 r = −0.204, p = 0.466 |
| Upper arm | 45.9 ± 14.5  | r = 0.781, p = 0.001 r = 0.232, p = 0.405 r = −0.185, p = 0.569 r = 0.540, p = 0.038 |
| Forearm   | 40.3 ± 14.9  | r = 0.840, p < 0.001 r = 0.364, p = 0.183 r = −0.239, p = 0.391 r = 0.621, p = 0.013 r = 0.746, p = 0.001 |
| Back      | 24.7 ± 5.9   | r = 0.286, p = 0.301 r = −0.172, p = 0.539 r = 0.382, p = 0.160 r = 0.244, p = 0.340 r = 0.053, p = 0.853 r = −0.035, p = 0.901 |
| Abdomen   | 16.9 ± 6.2   | r = 0.354, p = 0.195 r = 0.061, p = 0.830 r = 0.151, p = 0.590 r = −0.053, p = 0.852 r = 0.261, p = 0.348 r = 0.057, p = 0.841 r = 0.482, p = 0.069 |
| Thigh     | 21.0 ± 8.0   | r = 0.678, p = 0.006 r = 0.156, p = 0.579 r = 0.043, p = 0.878 r = 0.342, p = 0.212 r = 0.668, p = 0.005 r = 0.808, p < 0.001 r = −0.236, p = 0.398 r = −0.142, p = 0.614 |
| Calf      | 15.6 ± 3.6   | r = 0.559, p = 0.03 r = 0.369, p = 0.176 r = −0.246, p = 0.378 r = 0.394, p = 0.146 r = 0.385, p = 0.195 r = 0.67, p = 0.006 r = −0.355, p = 0.195 r = −0.131, p = 0.643 r = 0.566, p = 0.028 |

Participants are also included in study 1. The tactile stimulation (as described for study 1) was then applied to both arms, in randomized order. The participants rated the perceived eroticism, pleasantness and intensity of the stimulation. The effect of the hair on the ratings of touch perception was tested using 2-way ANOVAs with velocity and hair/depilated as within subject factors. The results showed that there was no significant main effect of hair on any of the ratings (eroticism: F[1, 10] = 0.227, p = 0.67; pleasantness: F[1, 10] = 0.006, p = 0.921, intensity: F[4, 40] = 0.131, p = 0.901). Furthermore, there were no significant interaction effects (hair by and velocity) on the ratings (eroticism: F[2, 179; 21, 789] = 0.219, p = 0.823 (Greenhouse-Geisser corrected), pleasantness: F[4, 40] = 0.227, p = 0.921, intensity: F[4, 40] = 1.594, p = 0.195).

Statistical Analysis. For both studies, statistical analysis was performed using IBM SPSS Statistics for Windows, Version 22.0 (IBM; Armonk, NY, USA). Demographic variables (age, weight, height and BMI) were compared between genders using t-tests. HFD was correlated to the weight and height of the participants. Further the HFD was compared between genders using a univariate analysis of variance. We included the weight and height as covariates in this model in order to control for the relation between HFD and gender.

For analysis of the touch ratings, the average value for every skin stroking velocity was determined from the 3 repetitions. Three repeated measures ANOVAs, with velocities (5) as within subject factors and gender (2) as between subject factor were used to analyze the ratings on pleasantness and intensity. Greenhouse-Geisser corrected in order to account for violations of sphericity.

Two main affective touch outcome variables were defined: The overall touch pleasantness/intensity was calculated as the mean of all touch pleasantness/intensity ratings. The pleasant touch awareness reflects the highest C-tactile specific pleasantness ratings and is calculated as the difference of pleasantness ratings between C-tactile optimized (3 cm/s) and non-optimized stroking (30 cm/s), weighted by the overall touch pleasantness. This calculation derived from the largest difference in ratings between C-tactile and non-C-tactile targeted touch experience in previous studies.\(^{15,16}\)

$$\text{pleasant touch awareness} = \frac{\text{pleasantness rating at 3 cm/s} - \text{pleasantness rating at 30 cm/s}}{\text{overall touch pleasantness}}$$

The relation between HFD and pleasant touch awareness and overall touch measures was tested using non-parametric correlations. The results of the eroticism ratings are available in the supplement. A potentially moderating effect of the weight and height was taken into account in an additional analysis. Therefore, a partial correlation between HFD and all touch variables was computed with the weight and height as control variable.

In study 2, the two-point discrimination threshold was additionally assessed in a non-parametric way and hence related to the participants’ sex and weight by Spearman correlation coefficient. Further, this threshold was compared between male and female participants using the Mann-Whitney U test and sex and weight were included in the gender-effect analysis by using general equation modelling (GEE), implemented in SPSS. The correlation between two-point discrimination threshold and HFD was further tested using Spearman correlation.
Combined Analysis of Study 1 and 2. To account for different anchor points used in the separate studies, ratings for perceived pleasantness were re-scaled to the scale used in study 2 using a linear transformation (10 rating points were added to ratings of pleasantness obtained in study 1 to transform from −10/10 to 0/20 scale). First, the participants of both studies were compared according to demographic criteria (Chi Square test) and age, weight and height (t-test), as well as according to all outcome variables (HFD, pleasant touch awareness, erotic touch awareness, overall pleasantness, overall eroticism, overall intensity; all with t-test).

HFD was correlated to the weight and height of the participants. The effect of gender on HFD was computed using a univariate analysis of variance with the weight and height as a covariate. HFD was further correlated to all touch perception variables, as reported for study 1.

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Acknowledgements
The studies were funded by a grant from the German Research Foundation (DFG; CR 479/1-1), and by a grant from the Swedish Research Council. We thank Dr Gerhard Ritschel for the kind assistance with the artwork. We thank Prof. Michael Kasper and PD Kathrin Barth from the Department of Anatomy, Dresden University of Technology, for their help with data assessment. We acknowledge support by the German Research Foundation and the Open Access Publication Funds of the TU Dresden.
Author Contributions
E.H.J. and J.B. share first authorship. H.B.W. and I.C. share senior authorship. J.W., H.B.W. and E.H.J. designed study 1, which was conducted by E.H.J. Study 2 was designed by I.C., K.W., H.O. and J.B. and the study was conducted by J.B. E.H.J., J.B., H.B.W. and I.C. analyzed the according data and wrote the main manuscript text. E.H.J. and J.B. prepared the figures. All authors reviewed the manuscript.

Additional Information
Supplementary information accompanies this paper at doi:10.1038/s41598-017-02308-9

Competing Interests: The authors declare that they have no competing interests.

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