Stroking hardness changes the perception of affective touch pleasantness across different skin sites

Check for updates

Jiabin Yu [a], Jiajia Yang [b,*], Yinghua Yu [b], Qiong Wu [b], Satoshi Takahashi [b], Yoshimichi Ejima [b], Jinglong Wu [b,c,**]

[a] Cognitive Neuroscience Laboratory, Graduate School of Natural Science and Technology, Okayama University, Okayama, 7008530, Japan
[b] Cognitive Neuroscience Laboratory, Graduate School of Interdisciplinary, Science and Engineering in Health Systems, Okayama University, Okayama, 7008530, Japan
[c] Shanghai University of Traditional Chinese Medicine, Shanghai, China

ABSTRACT

Human unmyelinated tactile afferents (CT afferents) in hairy skin are thought to be involved in the transmission of affective aspects of touch. How the perception of affective touch differs across human skin has made substantial progress; however, the majority of previous studies have mainly focused on the relationship between stroking velocities and pleasantness ratings. Here, we investigate how stroking hardness affects the perception of affective touch. Affective tactile stimulation was given with four different hardness of brushes at three different forces, which were presented to either palm or forearm. To quantify the physical factors of the stimuli (brush hardness), ten naïve, healthy participants assessed brush hardness using a seven-point scale. Based on these ten participants, five more participants were added to rate the hedonic value of brush stroking using a visual analogue scale (VAS). We found that pleasantness ratings over the skin resulted in a preference for light, soft stroking, which was rated as more pleasant when compared to heavy, hard stroking. Our results show that the hairy skin of the forearm is more susceptible to stroking hardness than the glabrous of the palm in terms of the perception of pleasantness. These findings of the current study extend the growing literature related to the effect of stroking characteristics on pleasantness ratings.

1. Introduction

Touch sensations are transmitted by different combinations of mechanoreceptors. The experience of touch leads to sensations that involve both discriminative and emotional aspects (McGlone et al., 2007). According to these theories, the experiences of touch are mediated by two separable dimensions, classified as sensory-discriminative and motivational-affective (Morrison et al., 2010). Although much more is known about the perception of discriminative touch, such as roughness, shape and vibration discrimination, little is known about affective touch, which plays a critically important role in interpersonal communication (Gallace and Spence, 2010).

It is widely accepted that human discriminative touch is mediated through low-threshold mechanoreceptors with large, myelinated A-beta (Aβ) fibers (Vallbo and Johansson, 1984; Bensmaia, 2008). In contrast, recent studies have suggested that unmyelinated, small-diameter, lower-threshold mechanoreceptive afferents (C-LTMRs), also called C tactile

or CT afferents, are involved in the transmission of affective aspects of touch (Olausson et al., 2002; McGlone et al., 2007; Loken et al., 2009; Liljencrantz and Olausson, 2014). There is no evidence for existence of CT afferents in the glabrous skin (Vallbo et al., 1999; Olausson et al., 2002; Loken et al., 2009; Olausson et al., 2010; McGlone et al., 2014; Perini et al., 2015), yet the phenomenon that glabrous skin touch perceived as pleasant is very common. In addition, previous studies have shown that sensory factors such as hardness (Rolls et al., 2003), temperature (Ackerley et al., 2014a), force and velocity (Loken et al., 2009; Ackerley et al., 2014b), contribute to pleasantness ratings of affective touch. Here, the focus of our research is to investigate the relationship between stroking hardness and affective touch over two different skin sites.

The majority of previous behavioral studies have focused on pleasantness ratings at different levels of stroking velocities over skin sites (Loken et al., 2009; Loken et al., 2011; Ackerley et al., 2014b); these studies have all consistently suggested that the glabrous skin of the palm

---

presents a flatter, inverted U-shaped stroking velocity-pleasantness rating profile compared to the hairy skin of the forearm. Previous functional magnetic resonance imaging (fMRI) studies (Olausson et al., 2002; Bjornsdotter et al., 2009) have shown that CT-targeted touch mainly projects to the insular cortex rather than the somatosensory cortices. The recent positron emission tomography (PET) study (McGlone et al., 2012) showed affective touch on the arm give significant activations of the posterior insular cortex and mid-anterior orbitofrontal cortex (OFC) in comparison to the palm, while the opposite contrast (touch on the arm minus touch on the palm) showed a significant activation of the somatosensory cortices. Further, the dissociation of insula function suggests posterior and anterior insula involvement in distinct yet interacting processes: coding physical stimulation and affective interpretation of touch by investigating brain responses to CT-targeted touch in the experience versus imagine conditions (Lucas et al., 2015). From these studies, stroking velocities also have different effects on the perception of affective touch on the palm and the forearm, and experiencing affective touch to arm and palm recruit either overlapping or distinct brain responses. We hypothesize that physical characteristics, particularly stroking hardness, may also have different effects on the perception of pleasantness from hairy and glabrous skin just like stroking velocities.

Here, a $2 \times 3 \times 4$ factorial experiment was designed, with the factors being 2 locations, 3 stroking forces and 4 stroking hardness grades. We investigated the relationship between stroking forces and affective touch over two different skin sites. Since the light touch seems suitable for human social interaction, we predicted that the light stroking force would be more pleasant than the heavy stroking force. We also wanted to investigate whether stroking hardness has a different effect on pleasantness ratings of affective touch on the hairy skin of the forearm and the glabrous skin of the palm. We predicted that the hairy skin of the forearm is more susceptible to stroking hardness than the glabrous of the palm in terms of the perception of affective touch pleasantness. We tested this hypothesis by contrasting the slope of the regression line between hardness and the perception of affective touch administered to the hairy skin of the forearm versus the glabrous skin of the palm.

2. Materials and methods

2.1. Experiment 1 (Measurement of brush hardness)

Experiment 1 was designed to measure the hardness of the brushes used in the affective touch experiment (experiment 2).

2.1.1. Participants

In total, 10 participants (5 males, Mean age 25.6 years, and 2.3 SD; 5 females, Mean age 26.6 years, and 2.4 SD) took part in the study. The study was approved by the ethics committee of the University of Okayama. All the participants were right-handed and given basic information about the experiment. Written informed consent was obtained from all the participants prior to their participation.

2.1.2. Experimental setting and procedure

After receiving a written explanation of the experiment, which included a description of the experimental setting and instructions on how to rate the stimuli, the temperature of the experimental room was adjusted to a suitable temperature by the air conditioner (Watanabe et al., 2012; Ackerley et al., 2014d). During the experiment, an accurate digital alarm clock with thermometer Sensor (BC247L, Seiko Co., Ltd., Japan) was placed within one meter of the participants, and the temperature was recorded every five minutes. The actual temperature of the experimental room was Mean $24 \pm$ SD 0.5 °C. The participants were then comfortably seated in an adjustable chair, and the fingers of each participant were wrapped in a piece of surgical tape to insure that the brush would not touch the participants' fingers during palm stimulation (Fig. 1). The participants naturally put their left hands or left forearms on a high-precision, portable, digital scale (hand: KD192, Tanita
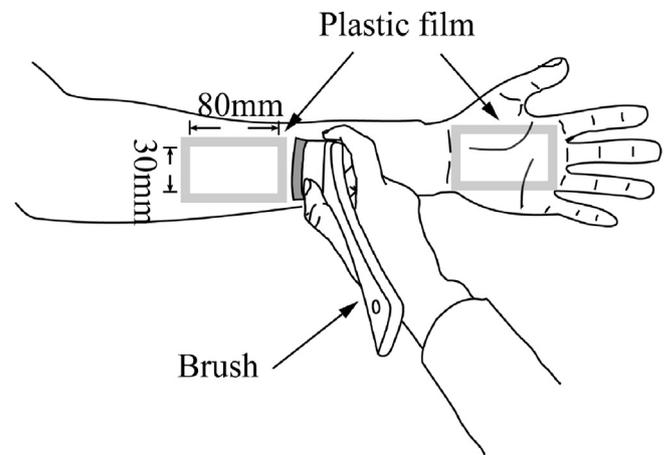

Fig. 1. Diagrammatic representations of the stroking stimuli. An assistant conducted the stimuli using a soft brush, and stroking forces were controlled by observing the display of electronic scales. A window (30×80 mm) in the plastic film exposed the skin to the moving brush and assured maintenance of a constant spatial relationship between the brush and the body part.

Corporation, Japan; forearm: CS-20KS, Custom Corporation, Japan) during palm or forearm stimulations. A baffle was used to shield the participants from seeing the tactile stimulation.

Stimulations were all made with four types of artist's flat, 50-mm-wide, watercolor brushes, each with different levels of hardness. Although the bristles are different materials (goat's hair, mixed wool, artificial wool, pig's hair) for all brushes, the bristles were wrapped in aluminum skin to insure that the bristles are all 20mm deep. To investigate the physical properties of the brushes, we took a 2×2 mm^2 area sample unit from the center of each brush bristle and then count the number of bristles in the sample. The number of bristles per unit area (1 mm^2) in the sample is approximately the density of the bristle. Subsequently, we took a sample of 100 bristles from the center of each brush bristle. In order to objectively investigate the diameter of the bristles, the diameters of the tip and middle of the 100 bristles were all measured using a high precision outside micrometer (M110-25, Mitutoyo Co., Ltd., Japan). The average tip/middle diameter of the sample is approximately the tip/middle diameter of the bristle. The physical parameters of the brushes are listed in Table 1.

The caress-like strokes were administered by a well-trained research experimenter on a palm/forearm to fingertip direction at a rate of

Table 1

Main physical properties of bristles.

Brush	Material	Density	Tip Diameter (μm) Mean ± SD	Middle Diameter (μm) Mean ± SD
Brush1	Fiber 100%	68	52.80 ± 13.58	94.42 ± 11.32
Brush2	PET 60%; PP 20%; Goat hair 20%	88	37.20 ± 13.22	70.17 ± 16.13
Brush3	Goat hair 50%; Chemical fiber 50%	75	72.79 ± 33.55	85.24 ± 33.41
Brush4	Pig hair 100%	33	73.99 ± 26.30	143.62 ± 22.01

The table shows the main physical properties of the brush bristles used in the experiment.
Material: the material of the bristles; PET: Polyethylene terephthalate, PP: Polypropylene; The number indicates the proportion of each component.
Density: the number of the bristles per 1 mm^2 area located in the center part of the brush bristles material.
Tip diameter: the mean ± SD diameter (μm) of the tip of 100 bristles located in the center part of the brush bristles material.
Middle diameter: the mean ± SD diameter (μm) of the middle (equidistant from bristle tip and root) of 100 bristles located in the center part of the brush bristles material.

approximately 3 cm/s, a CT-optimal stroking speed (Loken et al., 2009). The participants' hands (forearms) were fixed during the experiment to prevent movement on the weighing platform of the high-precision digital scale, thereby insuring the highest possible accuracy. The experimenter applied different forces to the brushes and achieved three different desired forces 1N, 1.7N, 3N by observing the display on the high-precision digital scale. Despite the error, the experimenter controlled the error below 0.15N as much as possible. We collected the actual exerted forces of one participant at the three time points (the starting time point, the intermediate time point, and the end time point) in each brush stroke using a high-speed camera (HDE-CX630V, Panasonic Corporation, Japan). Finally, we plotted the figure of the average actual forces corresponding to the average expected forces and gave the error bars of the standard deviation (Fig. 2).

Tactile sensations were explored over the following two skin sites: left palm (in the center, equidistant from the bottom of the third finger and the wrist) and left forearm (on the volar side, equidistant from the wrist and elbow) (Ackerley et al., 2014b). In addition, a window (30 × 80 mm) in the plastic film exposed the skin to the moving brush and assured maintenance of a constant spatial relationship between the brush and the body part. Following each brush stroke, the participants were instructed to rate the sensation on two subsequently presented seven-point Likert-like scales (Guest et al., 2012; Sakamoto and Watanabe, 2017), using a custom-made scale, which was fixed to a table in front of the participant. In the first Likert-like scale, the participants were asked to answer the question: "how hard was the brush?". The rating scale consisted of 7 choices (ranging from 1 = extremely soft to 7 = extremely hard). In the second Likert-like scale, which occurred directly after the first, the participants were asked to answer the question: "how rough was the brush?". The rating scale consisted of 7 choices (ranging from 1 = extremely smooth to 7 = extremely rough). As the study was conducted in Japan, the descriptors of the scales were presented in Japanese. Therefore, the responses were also recorded in Japanese and subsequently translated into English. The translation was carried out independently by two fluent Japanese-speaking, native British individuals, and the descriptors were also compared to dictionary definitions of the words. It was also back-translated into Japanese by an individual, who knew nothing about the original Japanese descriptors. Since the back-translated to Japanese corresponded to the original Japanese descriptors, the translation into English was considered satisfactory.
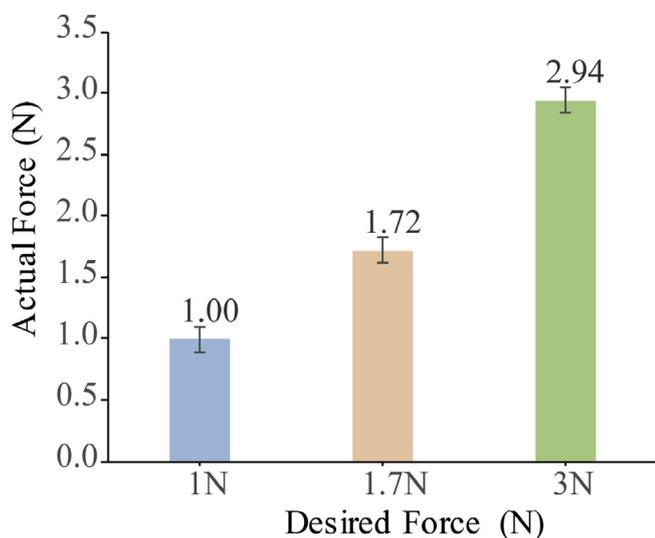
Although we provided two items (roughness, hardness) for the participants to answer, the main focus of the research was to investigate the influence of hardness on pleasantness ratings of gentle stroking. The participants had 5 s to complete both Likert-like scales. Therefore, this experiment consisted of a 2 × 3 × 4 design, where the Site condition had two levels (palm, forearm), the Force condition had three levels (1 N, 1.7 N, 3 N), and the Hardness condition had four levels. Each trial was repeated five times in a pseudo-random order.

2.1.3. Statistical analysis

The average raw scores for hardness ratings at different stimulation conditions have been shown in Fig. 3. Since the basic data obtained from measurements using an ordinal scale were not normally distributed, the transformation of the ordinal scale to interval scale should be done before parametric statistics. In addition, although the scale values of the stimuli were defined as projected upon a psychological continuum, the method of equal-appearing intervals makes an implausible assumption of "equal intervals". Therefore, all the data were analyzed using the method of successive interval (MSI) (Edwards, 1952; Blischke et al., 1975; Matthews et al., 2002). In the study, n = 12 stimuli were rated by 10 participants on a 7-point Likert-like scale ranging from extremely soft, to neutral, to extremely hard. From the proportion of each option, the cumulative distributions for each stimulus are given in Table 2.

Assuming that the judgements for each stimulus are normally distributed on a psychological continuum, the boundaries of categories can be expressed as standard normal deviates. The area under the standard normal curve is divided into 7 sections according to the proportion of each option, and the area in each section is then obtained from the frequency of choice. If the table of cumulative proportion is entered with value p_{jk}, the corresponding standard normal deviate X_{jk} will be the upper limit of the kth category over the rating stimulus j. Stimulus 2, for example, provides estimates of the upper limits of categories 1, 2, 3, and 4. Expressed as standard normal deviates, these upper boundaries are -0.99, 0.52, 2.05, and 2.33, respectively. It is important to note that the lower limit of category 1 and the upper limit of category 7 are indeterminate because they are the endpoints. Let Y_{jk} be the density value corresponding to the upper limit of the kth category. $Y_{j(k-1)}$ can be understood as the density value corresponding to the lower limit of the kth

Fig. 2. The actual exerted mean forces at different desired forces. The y-axis represents the actual exerted mean force corresponding to the desired force. Corresponding to the desired force of 1N, 1.7N, 3N, the actual exerted mean force is 1N, 1.72N, and 2.94N, respectively. The error bars represent the standard deviation (SD) of the means.
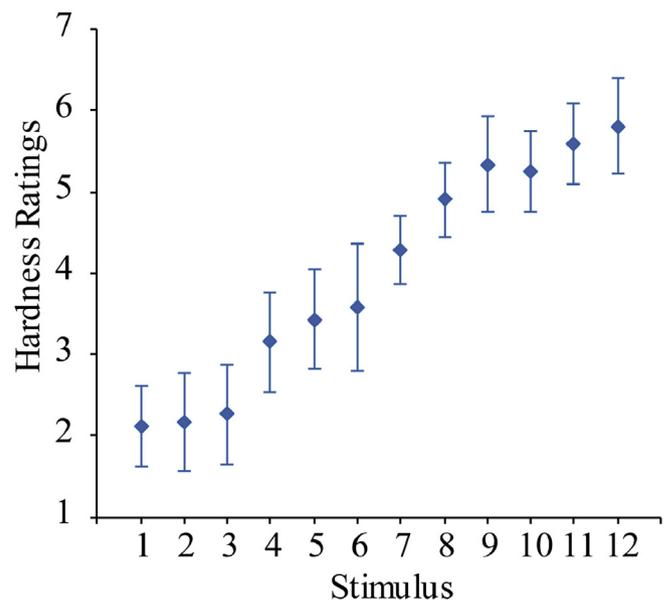

Fig. 3. The average raw scores for hardness ratings at different stimulation conditions. The x-axis represents the 12 different stimulus conditions (3 force × 4 hardness), which has been stated in Table 2. The y-axis is the average raw scores for stroking hardness in context of a seven-point scale used to elicit answers. Error bars correspond to ±SD.

Table 2
Cumulative proportion of judgement for stimuli.

Stimulus	Rating Category						
	1	2	3	4	5	6	7
1. f1h1	0.17	0.76	0.98	0.99	0.99	1.00	1.00
2. f2h1	0.16	0.70	0.98	0.99	1.00	1.00	1.00
3. f3h1	0.13	0.65	0.96	1.00	1.00	1.00	1.00
4. f1h2	0.01	0.28	0.69	0.89	0.98	1.00	1.00
5. f2h2	0.01	0.17	0.59	0.82	0.98	1.00	1.00
6. f3h2	0.01	0.18	0.52	0.73	0.97	1.00	1.00
7. f1h3	0.01	0.02	0.16	0.60	0.92	1.00	1.00
8. f2h3	0.00	0.00	0.05	0.34	0.73	0.98	1.00
9. f3h3	0.00	0.01	0.03	0.14	0.54	0.94	1.00
10. f1h4	0.00	0.00	0.03	0.16	0.62	0.95	1.00
11. f2h4	0.00	0.00	0.02	0.04	0.42	0.93	1.00
12. f3h4	0.00	0.00	0.01	0.04	0.28	0.84	1.00

Table 2 **is an n × r matrix, where n is the number of stimuli and r is the number of rating categories.** Let the general element of Table 1 be p_{jk}, which shows the proportion of rating a given stimulus j in the kth category or below; $1 - p_{jk}$ is the proportion of rating stimulus j above the kth category. f1 = force 1N, f2 = force 1.7N, f3 = force 3N. h1 = hardness of brush 1, h2 = hardness of brush 2, h3 = hardness of brush 3, and h4 = hardness of brush 4. Stimulus 1 of f1h1 indicates the stroke of brush 1 under downward force 1N. Similarly, stimulus 12 of f3h4 indicates the stroke of brush 4 under downward force 3N.

category. In particular, the density value Y_{j0}, corresponding to the lower limit of category 1, and the density value Y_{j7}, corresponding to the upper limit of category 7, are expressed as 0. All the subsequent calculations are based on the data in Table 2. Therefore, the scale value (SV) for each category will be computed by

$$SV_k = \frac{Y_{k-1} - Y_k}{P_k - P_{k-1}}$$

where SV_k is the scale value of category k. Y_k is the density value corresponding to the upper limit of category k. Y_{k-1} is the density value corresponding to the lower limit of category k. P_k is the cumulative proportion of category k. The denominator $P_k - P_{k-1}$ is the proportion of category k. When is 0, the scale value will be ignored. The scale values of each category of the other stimuli are obtained in the same manner; thus, the means of all the stimuli will be defined as the scale values of each category. These scale values for each category are -2.19, -1.29, -0.87, 0, 0.40, 1.45, and 1.98. To transform SV_1 (the scale value for category 1) so that it equals 1, 3.19 needs to be added. This same amount is added to each of the other SV categories as well. The final SVs will be 1.00, 1.90, 2.31, 3.18, 3.58, 4.64, and 5.17.

After obtaining the final SV, the ordinal scale will be changed to the distance (interval) scale. Brush hardness can be obtained by calculating the normalized basic data and are 1.91, 2.66, 3.66, and 4.17. From Table 1, we found that stroking hardness was not linearly related to the density or the tip/middle diameter of the bristles.

2.2. Experiment 2 (Ratings of pleasantness)

To determine how stroking hardness affects pleasantness ratings from skin sites at different levels of stroking force, we conducted the second experiment. Here, stroking hardness was measured using a seven-point Likert-like scale in Experiment 1.

2.2.1. Participants

Fifteen healthy participants (8 males, Mean age 26.9 years, and 2.6 SD; 7 females, Mean age 26.6 years, and 2.4 SD) were recruited from Okayama University. Eight participants were male. Ten of the participants took part in Experiment 1. The study was approved by the ethics committee of the University of Okayama. All the participants were right-handed and given basic information about the experiment, and written informed consent was obtained from all the participants prior to their

participation.

2.2.2. Experimental setting and procedure

The experimental setting and procedure of Experiment 2 were identical to Experiment 1 in terms of the factorial design. Experiment 2 also consisted of a 2 × 3 × 4 design, where the Site condition had two levels (palm and forearm), the Force condition had three levels (1 N, 1.7 N, 3 N), and the Hardness condition had four levels (1.91, 2.66, 3.66, and 4.17). Following each brush stroke, the participants were instructed to rate the pleasantness of the brushing experience using a visual analogue scale (VAS) placed next to the right hand, ranging from -10 (unpleasant) over a neutral (0) midpoint to 10 (pleasant).

The participants were required to rate the pleasantness of the stimulation with a 10 s response interval. Each trial was repeated twenty times per skin site (palm/forearm) using brushes of different hardness with different stroking forces in a pseudo-random order. The data from each participant were collected over four sessions conducted on different days. Each session lasted for approximately 30 min.

2.2.3. Statistical analysis

All the statistical data were analyzed using SPSS (SPSS Statistics, Version 17; IBM, Armonk, NY). Significance was obtained at the p < 0.05 level, with up to three significant figures. The raw average scores for pleasantness ratings from the palm and forearm was shown in Fig. 4A-B. The data were first tested for normality of distribution using one-sample Kolmogorov-Smirnov tests. From the test results, the tactile pleasantness ratings were found to be normally distributed (Kolmogorov-Smirnov test p > 0.05) and were analyzed using parametric tests. The mean tactile pleasantness data were analyzed using a repeated-measures analysis of variance (ANOVA) with 3 within-subject factors: site (arm and forearm), force (1 N, 1.7 N, and 3 N), and hardness (1.91, 2.66, 3.66, and 4.17). Descriptive statistics were analyzed, and a full factorial model was used to explore the factors and the factor interactions. If the assumption of sphericity was violated in the Mauchly's sphericity test, the Greenhouse-Geisser (G-G) correction coefficient epsilon was used to correct the degrees of freedom, and P-values were then recalculated. Further, the main effects of each factor were compared, and post hoc tests were conducted to contrast the different levels of the factors by using Bonferroni-corrected pairwise comparisons of the estimated marginal means, controlling for multiple comparisons. Simple-simple main effects were further conducted to reveal whether there were significant differences between stimulation sites (palm/forearm) for pleasantness ratings under a combination of the factors force and hardness. Finally, to investigate the relationship between tactile pleasantness ratings and stroking forces, linear regression analyses were performed. The pleasantness of a stimulus was defined as the dependent variable, with stroking forces as independent variables.

3. Results

The tactile pleasantness data were analyzed using repeated measures ANOVA to reveal significant differences in the pleasantness ratings for different skin sites, stroking forces and stroking hardness. Main effects of skin sites ($F_{1,14} = 7.43, p = 0.016$), stroking forces ($F_{1.11,15.50} = 28.23, p < 0.001$) and stroking hardness ($F_{1.17,16.41} = 38.52, p < 0.001$) were found. The main effects can be seen in Fig. 4A-B, where tactile stimuli with light stroking hardness to be rated as more significantly pleasant than the other stimuli at high stroking hardness; a light stroking force was rated as more significantly pleasant than a heavy stroking force of the skin sites.

There were significant interaction effects between the skin sites and stroking forces ($F_{1.42,19.83} = 7.47, p = 0.007$) as well as between the skin sites and stroking hardness ($F_{1.91,26.79} = 11.92, p < 0.001$). There was also a significant interaction effect between stroking force and hardness ($F_{6,84} = 6.55, p < 0.001$). Although there was no significant three-way interaction among skin sites, stroking forces and stroking hardness, main two-
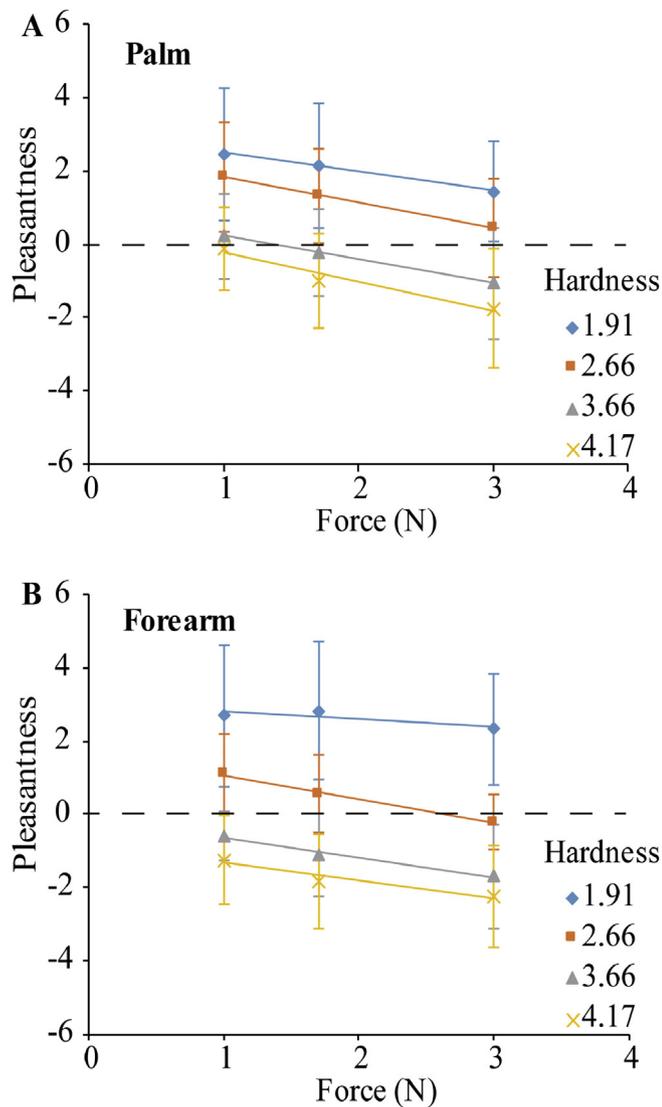
Fig. 4. Pleasantness ratings at different stroking forces with different brush hardness levels over skin sites. The y-axis (A-B) is the raw average scores for pleasantness ratings from the palm (A) and forearm (B) in context of the ratings scale (-10, 10) used to elicit answers. Main significant effects were found for all factors, including stroking forces ($p < 0.001$), stroking hardness ($p < 0.001$), and skin sites ($p = 0.016$). The lighter forces were rated as more significantly pleasant compared to heavier stroking forces for all skin sites. Higher stroking hardness led to less pleasantness ratings than lower stroking hardness for all skin sites. Error bars correspond to ±SD.

way interaction effects showed significance, and there were multiple levels for each factor; thus, extensive analyses (simple-simple main effects) were deemed necessary to uncover the influences of stroking hardness on the skin sites among stroking forces, and to detect subtle effects over different factor levels.

Extensive analyses showing the main effect of skin site at each level of stroking force were shown in Fig. 5A-C, where stroking hardness has a different effect on the perception of pleasantness for the palm and the forearm. We found no significant main effect of skin site at the level of stroking hardness 1.91, but there were significant main effects of skin site at levels of stroking hardness of 2.66 ($p = 0.009$), 3.66 ($p = 0.003$), and 4.17 ($p = 0.001$) for the 1N level of stroking force. For the level of stroking force 1.7N, there were significant main effects of skin site at all levels of stroking hardness of 1.91 ($p = 0.031$), 2.66 ($p = 0.007$), 3.66 ($p = 0.003$), and 4.17 ($= 0.001$). Intriguingly, significant main effects of skin site were found at the levels of stroking hardness of 1.91 ($p = 0.024$),

3.66 ($p = 0.018$), and 4.17 ($p = 0.021$), but no significant main effect of skin site at the level of stroking hardness 2.66 was found for the 3N level of stroking force.

Linear regression analyses were conducted to explore the relationship between tactile pleasantness ratings and stroking forces, per stroking hardness. For the palm skin site, all the linear regressions were significant: stroking hardness of 2.66 ($R^2 = 0.158$, $p = 0.007$), stroking hardness of 3.66 ($R^2 = 0.152$, $= 0.008$), and stroking hardness of 4.17 ($R^2 = 0.197$, $p = 0.002$). For the forearm skin site, the following linear regressions were significant: stroking hardness of 2.66 ($R^2 = 0.239$, $p = 0.001$), stroking hardness of 3.66 ($R^2 = 0.150$, $p = 0.009$), and stroking hardness of 4.17 ($R^2 = 0.089$, $p = 0.046$). No significant linear regression was found at a stroking hardness of 1.91 for both skin sites.

4. Discussion

In this study, we investigated the effect of stroking hardness on pleasantness ratings by stroking four different brushes on two different skin sites using three stroking forces. In terms of pleasantness ratings, the hairy skin of the forearm is more susceptible to stroking hardness than the glabrous skin of the palm, independent of the effects of forces. This result suggests that pleasantness ratings from hairy skin decrease at a faster rate compared to glabrous skin as stroking hardness becomes harder and that there is an interaction between stroking hardness and stroking sites on ratings of pleasantness (Fig. 5). Adding to previous research on affective touch (Loken et al., 2009; Loken et al., 2011; Ackerley et al., 2014b; Fairhurst et al., 2014), there are different effects of stroking hardness on the perception of pleasantness for palm and forearm stimulation.

The main finding in the current study is that the hairy skin of the forearm is more susceptible to stroking hardness than the glabrous skin of the palm in the range perceived as affective touch. It is well known that CT afferents involved in the transmission of affective tactile signals are exclusively innervated in hairy skin (e.g., the forearm) (Loken et al., 2009), and the stroking velocity-pleasantness profile has previously been confirmed to be different between glabrous and hairy skin (Loken et al., 2009; Morrison et al., 2011b; Ackerley et al., 2014b). Previous fMRI studies (Bjornsdotter et al., 2009; McGlone et al., 2012; Gordon et al., 2013; Voos et al., 2013) have shown that CT-targeted touch on the forearm mainly project onto the insular cortex when compared to the palm, while the opposite contrast (touch on the palm minus touch on the arm) showed a significant activation of somatosensory cortices. We speculate that these differential effects may be related to not only the distinct brain responses, but also cutaneous receptors responding to skin deformation. In line with previous studies (McGlone et al., 2012; Ackerley et al., 2014c; Klocker et al., 2014), our results suggested that gentle skin stroking of the glabrous skin, where the unmyelinated CT afferents are never found, is also perceived as pleasant. Hence, Aβ fibers (that are present in both the hairy and glabrous skin) also seem to play a key role in the transmission of the affective aspects of touch by conveying discriminative information (e.g., concerning the speed and force of stimulation (McGlone et al., 2007; McGlone et al., 2014)) to the brain.

Previous studies have demonstrated that CT afferent discharges prefer gentle touch with low indentation forces (Wessberg et al., 2003; McGlone et al., 2007; Loken et al., 2009). To make the experimental results more objective, we also considered stroking forces as a factor in the experimental design. It should be noted that stroking hardness is a psychological perception based on complex interaction between stiffness of brush, its endpoint characteristics, sheer forces in the brush filament and skin indentation. However, a significant interaction between stroking force and hardness was found, which indicated that force and hardness were not similar dimensions despite inseparable. Therefore, it was considered that the subjects tended to evaluate the hardness of brushes according to the characteristics of bristles, despite the contribution of the exerted downward forces to hardness ratings. Our results suggest that the

A

B

C
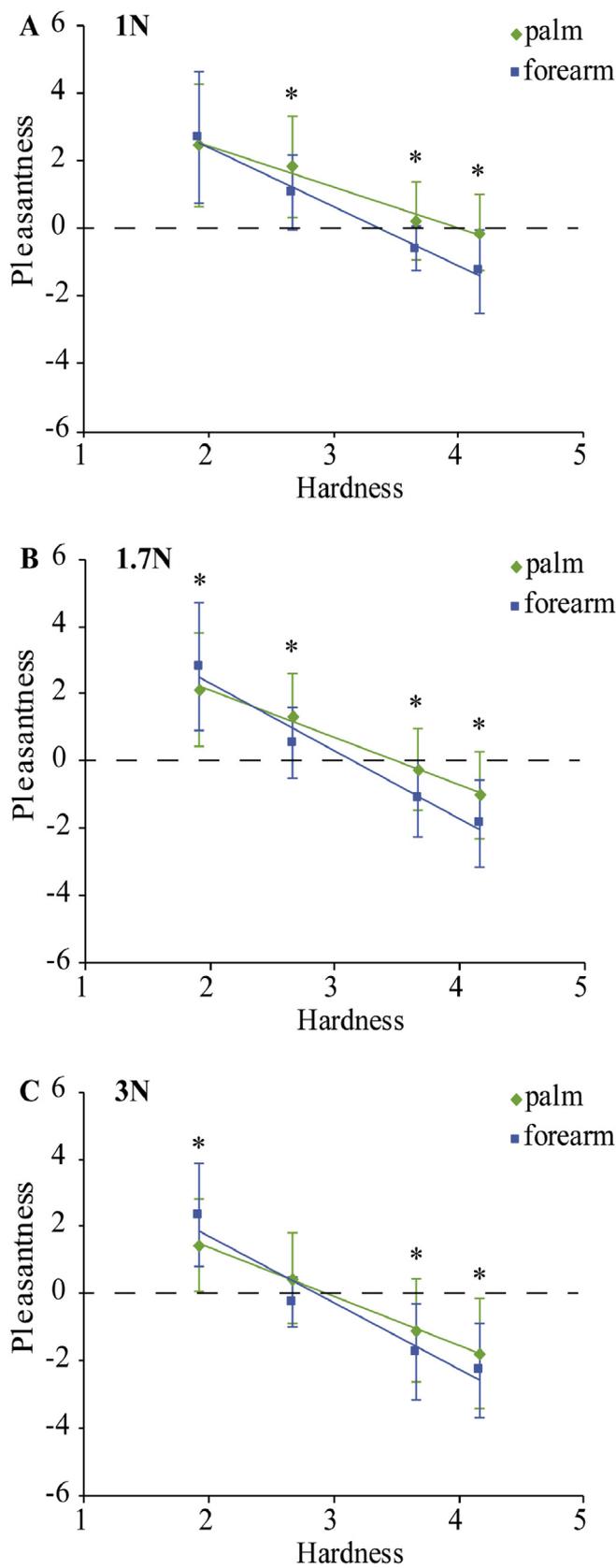
(caption on next column)

light stroking forces were considered more significantly pleasant when compared to heavy stroking forces. A previous study of passive fingertip (glabrous skin) stimulation showed that the average roughness of touch plates and friction force were negatively related to pleasantness and that there was no significant correlation between the force of stimulus application or stimulus temperature and pleasantness (Klocker et al., 2014). This result indicates that the perception of pleasantness in response to affective touch can be modulated by the physical properties of stimuli as well as by its force and velocity profile. Furthermore, we found that pleasantness ratings from the hairy skin of the forearm are more sensitive than the glabrous skin of the palm and that an interaction was present between stroking hardness and stroking sites independent of the effects of force. The differential effect of stroking hardness on the perception of affective touch to the palm and forearm may be attributed to several factors, such as the type of skin (e.g. the differential presence of CT afferents between glabrous skin and hairy skin), its innervation and central signal extraction mechanisms. Because the difference between glabrous and hairy skin is divided not only by CT afferents, but also other factors. For instance, myelinated fibers in the hairy skin are irregularly distributed around the follicles in a high density compared to their homogeneous population of glabrous skin. These nerve fibers' are entangled in glabrous skin, but straight and stretched in hairy skin (Provitera et al., 2007). In addition, Meissner corpuscles are uniquely present in the glabrous skin to encoding discriminative aspects of touch, while the hair follicle endings in the hairy play a role in this aspect. These difference may also result in different responses to stimulation of glabrous and hairy skin.

Another possibility of affecting the perception of affective touch is roughness. A Hard–Soft dimension has also been identified to be an important tactile attribute (Guest et al., 2011). A passive fingertip stimulation study indicated that the mean roughness of skin-stimulus interface was negatively correlated with pleasantness (Klocker et al., 2014). In addition, it has been found that the smooth brush and fur were rated as significantly more pleasant than the rough sandpaper (Ackerley et al., 2014c). However, it is difficult for the present study to dissociate the influences of hardness and roughness on the perception of affective touch, and then omit limitation of the study. Thus, dissociating the influences of hardness and roughness on the perception of affective touch is one of future research. A second issue is the hand dominance. Despite extensive studies on handedness regarding the discrimination aspects of touch, it is still unknown whether dominant hand affects the perception of affective touch. In many previous studies (Bjornsdotter et al., 2009; Loken et al., 2011; Morrison et al., 2011a), tactile affective stimulation has been applied to either hand, but it does not mean that the emotional perception of touch is not affected by hand dominance. Therefore, the issue of hand dominance also needs further examination in future studies of affective touch.

These findings of the current study extend the growing literature related to the effect of stroking characteristics on pleasantness ratings and show that the hairy skin of the forearm is more susceptible to stroking hardness than the glabrous skin of the palm. However, despite their different innervations, there were many similarities in perception

Fig. 5. The effect of skin site on pleasantness ratings for different levels of stroking hardness. The y-axis (A-C) is the raw average scores for pleasantness ratings from the palm and forearm in context of the rating scale (-10, 10) used to elicit answers. There were main effects of skin site on a stroking hardness of 2.66, hardness of 3.66, and hardness of 4.17 for the level of stroking force (A) 1N. For the level of stroking force (B) 1.7N, there were significant main effects of skin site at all levels of stroking hardness. And for the level of stroking force (C) 3N, significant main effects of skin site were found on a stroking hardness of 1.91, hardness of 3.66, and hardness of 4.17 (* indicates significant differences, $p < 0.05$). Furthermore, pleasantness decreased at a faster rate for stroking over the forearm compared to over the palm as stroking hardness becomes harder. Error bars correspond to ±SD.

between the forearm and the palm, which needs further examination in future studies. In addition, our experiment only investigated two stroking sites on the palm and forearm; therefore, there are limitations in explaining the differential effects between hairy and glabrous skin. The experiment was also conducted as a behavioral one, making it difficult to attribute the affective feelings of hairless skin to the top-down mechanism. Hence, further studies are needed to incorporate more stroking sites into the experimental design and to extend fMRI approaches to the experiments to better investigate the top-down mechanism.

Declarations

Author contribution statement

Jiabin Yu: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Jiajia Yang: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

Yinghua Yu, Qiong Wu, Satoshi Takahashi: Analyzed and interpreted the data.

Yoshimichi Ejima, Jinglong Wu: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data.

Funding statement

Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

References

Vallbo, A.B., Johansson, R.S., 1984. Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. Hum. Neurobiol. 3 (1), 3–14.

Ackerley, R., Backlund Wasling, H., Liljencrantz, J., Olausson, H., Johnson, R.D., Wessberg, J., 2014a. Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. J. Neurosci. 34 (8), 2879–2883.

Ackerley, R., Carlsson, I., Wester, H., Olausson, H., Backlund Wasling, H., 2014b. Touch perceptions across skin sites: differences between sensitivity, direction discrimination and pleasantness. Front. Behav. Neurosci. 8, 54.

Ackerley, R., Saar, K., McGlone, F., Backlund Wasling, H., 2014c. Quantifying the sensory and emotional perception of touch: differences between glabrous and hairy skin. Front. Behav. Neurosci. 8, 34.

Ackerley, R., Wasling, H.B., Liljencrantz, J., Olausson, H., Johnson, R.D., Wessberg, J., 2014d. Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. J. Neurosci. 34 (8), 2879–2883.

Bensmaia, S.J., 2008. Tactile intensity and population codes. Behav. Brain Res. 190 (2), 165–173.

Bjornsdotter, M., Loken, L., Olausson, H., Vallbo, A., Wessberg, J., 2009. Somatotopic organization of gentle touch processing in the posterior insular cortex. J. Neurosci. 29 (29), 9314–9320.

Blischke, W.R., Bush, J.W., Kaplan, R.M., 1975. Successive intervals analysis of preference measures in a health status index. Health Serv. Res. 10 (2), 181–198.

Edwards, A.L., 1952. The scaling of stimuli by the method of successive intervals. J. Appl. Psychol. 36 (2), 118.

Fairhurst, M.T., Loken, L., Grossmann, T., 2014. Physiological and behavioral responses reveal 9-month-old infants' sensitivity to pleasant touch. Psychol. Sci. 25 (5), 1124–1131.

Gallace, A., Spence, C., 2010. The science of interpersonal touch: an overview. Neurosci. Biobehav. Rev. 34 (2), 246–259.

Gordon, I., Voos, A.C., Bennett, R.H., Bolling, D.Z., Pelphrey, K.A., Kaiser, M.D., 2013. Brain mechanisms for processing affective touch. Hum. Brain Mapp. 34 (4), 914–922.

Guest, S., Dessirier, J.M., Mehrabyan, A., McGlone, F., Essick, G., Gescheider, G., et al., 2011. The development and validation of sensory and emotional scales of touch perception. Atten. Percept. Psychophys. 73 (2), 531–550.

Guest, S., Mehrabyan, A., Essick, G., Phillips, N., Hopkinson, A., Mcglone, F., 2012. Physics and tactile perception of fluid-covered surfaces. J. Texture Stud. 43 (1), 77–93.

Klocker, A., Oddo, C.M., Camboni, D., Penta, M., Thonnard, J.L., 2014. Physical factors influencing pleasant touch during passive fingertip stimulation. PLoS One 9 (7). ARTN e101361.

Liljencrantz, J., Olausson, H., 2014. Tactile C fibers and their contributions to pleasant sensations and to tactile allodynia. Front. Behav. Neurosci. 8, 37.

Loken, L.S., Wessberg, J., Morrison, I., McGlone, F., Olausson, H., 2009. Coding of pleasant touch by unmyelinated afferents in humans. Nat. Neurosci. 12 (5), 547–548.

Loken, L.S., Evert, M., Wessberg, J., 2011. Pleasantness of touch in human glabrous and hairy skin: order effects on affective ratings. Brain Res. 1417, 9–15.

Lucas, M.V., Anderson, L.C., Bolling, D.Z., Pelphrey, K.A., Kaiser, M.D., 2015. Dissociating the neural correlates of experiencing and imagining affective touch. Cerebr. Cortex 25 (9), 2623–2630.

Matthews, J., Berry, G., Armitage, P., 2002. Statistical Methods in Medical Research. Blackwell Science, Oxford.

McGlone, F., Vallbo, A.B., Olausson, H., Loken, L., Wessberg, J., 2007. Discriminative touch and emotional touch. Can. J. Exp. Psychol. Rev. Canad. Psychiatr. Exp. 61 (3), 173–183.

McGlone, F., Olausson, H., Boyle, J.A., Jones-Gotman, M., Dancer, C., Guest, S., et al., 2012. Touching and feeling: differences in pleasant touch processing between glabrous and hairy skin in humans. Eur. J. Neurosci. 35 (11), 1782–1788.

McGlone, F., Wessberg, J., Olausson, H., 2014. Discriminative and affective touch: sensing and feeling. Neuron 82 (4), 737–755.

Morrison, I., Loken, L.S., Olausson, H., 2010. The skin as a social organ. Exp. Brain Res. 204 (3), 305–314.

Morrison, I., Bjornsdotter, M., Olausson, H., 2011a. Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. J. Neurosci. 31 (26), 9554–9562.

Morrison, I., Loken, L.S., Minde, J., Wessberg, J., Perini, I., Nennesmo, I., et al., 2011b. Reduced C-afferent fibre density affects perceived pleasantness and empathy for touch. Brain 134 (Pt 4), 1116–1126.

Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B.G., Starck, G., et al., 2002. Unmyelinated tactile afferents signal touch and project to insular cortex. Nat. Neurosci. 5 (9), 900–904.

Olausson, H., Wessberg, J., Morrison, I., McGlone, F., Vallbo, A., 2010. The neurophysiology of unmyelinated tactile afferents. Neurosci. Biobehav. Rev. 34 (2), 185–191.

Perini, I., Olausson, H., Morrison, I., 2015. Seeking pleasant touch: neural correlates of behavioral preferences for skin stroking. Front. Behav. Neurosci. 9, 8.

Provitera, V., Nolano, M., Pagano, A., Caporaso, G., Stancanelli, A., Santoro, L., 2007. Myelinated nerve endings in human skin. Muscle Nerve 35 (6), 767–775.

Rolls, E.T., O'Doherty, J., Kringelbach, M.L., Francis, S., Bowtell, R., McGlone, F., 2003. Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. Cerebr. Cortex 13 (3), 308–317.

Sakamoto, M., Watanabe, J., 2017. Exploring tactile perceptual dimensions using materials associated with sensory vocabulary. Front. Psychol. 8. Artn 569.

Vallbo, A.B., Olausson, H., Wessberg, J., 1999. Unmyelinated afferents constitute a second system coding tactile stimuli of the human hairy skin. J. Neurophysiol. 81 (6), 2753–2763.

Voos, A.C., Pelphrey, K.A., Kaiser, M.D., 2013. Autistic traits are associated with diminished neural response to affective touch. Soc. Cogn. Affect. Neurosci. 8 (4), 378–386.

Watanabe, N., Miyazaki, S., Mukaino, Y., Hotta, H., 2012. Effect of gentle cutaneous stimulation on heat-induced autonomic response and subjective pain intensity in healthy humans. J. Physiol. Sci. 62 (4), 343–350.

Wessberg, J., Olausson, H., Fernstrom, K.W., Vallbo, A.B., 2003. Receptive field properties of unmyelinated tactile afferents in the human skin. J. Neurophysiol. 89 (3), 1567–1575.