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Short communication

Vicarious ratings of social touch reflect the anatomical distribution & velocity tuning of C-tactile afferents: A hedonic homunculus?

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HIGHLIGHTS

- Vicarious ratings of seen touch match the velocity tuning of C-Tactile afferents.
- Preferences reflect the hypothesised anatomical distribution of C-Tactile afferents.
- People recognise the specific rewarding value of C-Tactile afferent activating touch.

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ABSTRACT

A subclass of C-fibres, C-tactile afferents (CTs), have been discovered which respond preferentially to low force/velocity stroking touch, that is typically perceived as pleasant. Molecular genetic visualization of these low-threshold mechanosensitive C-fibres (CLTMs) in mice revealed a denser distribution in dorsal than ventral thoracic sites, scattered distal limb innervation and a complete absence from glabrous paw skin (Liu et al., 2007). Here we used third-party ratings to examine whether affective responses to social touch reflect the anatomical distribution and velocity tuning of CTs. Participants viewed and rated a sequence of video clips depicting one individual being touched by another at different skin sites and at 3 different velocities (static, 3 cm/s, 30 cm/s). Immediately after viewing each clip participants were asked to rate how pleasant they perceived the touch to be. Vicarious preferences matched the previously reported anatomical innervation density of rodent CLTMs, with touch on the back being rated significantly more pleasant than any other location. Furthermore, in contrast to all other skin sites, CT optimal (3 cm/s) touch on the palm of the hand was not preferred to static touch, consistent with the anatomical absence of CTs in glabrous skin. Our findings demonstrate that humans recognise the specific rewarding value of CT optimal caressing touch and their preferences reflect the hypothesised anatomical distribution of CTs.

1. Introduction

Tactile interactions are recognised as being central to the formation and maintenance of social bonds and thus to psychological wellbeing [1]. Recently, a subclass of cutaneous unmyelinated low threshold mechanoreceptors has been identified and characterised in human skin. Named C-tactile afferents (CTs), they respond preferentially to low force, skin temperature, stroking touch [2,3]. Microneurography studies have shown that CTs are velocity tuned, responding optimally to a stimulus moving over their receptive field at between 1 and 10 cm/s, with discharge frequencies that strongly correlate with subjective ratings of stimulus pleasantness as measured psychophysically [4]. Neurally, gentle stroking touch, applied at CT optimal velocities to hairy skin produces selective activation in posterior insula and orbitofrontal cortices [5,6]. Thus, in common with other C-fibers signaling pain and itch, their projection to affective brain regions is consistent with a role in signaling the emotional value rather than discriminative quality of touch.

Functionally, it has been proposed that CTs form the first stage of encoding socially relevant and rewarding tactile interactions resulting from affiliative behaviours [7,8]. In support of their social

Abbreviations: CTs, C-tactile afferents; CLTMS, C-low threshold mechanoreceptors; NAC, nucleus accumbens; ASD, autism spectrum disorder; S1, Primary somatosensory cortex.

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relevance, a recent observational study reported that, when asked to caress either their partner or their infant, people spontaneously used stroking velocities within the CT optimal range; this was not the case in a non-social context [9]. Evidence for the specific rewarding value of CT activating touch comes from rodent studies. For example, selective activation of C-fibre low-threshold mechanoreceptors (CLTMs) – the rodent equivalent of CTs – using pharmacogenetics, has been found to promote the formation of conditioned place preference [10]. Also, stroking touch applied to the hairy skin of rats at CT optimal velocities elicited dopamine release within the nucleus accumbens (NAC) [11]. Suggestive of an anatomical specificity to the distribution of CTs, stroking applied to the back elicited a significantly greater dopamine response than stoking the limbs.

In support of this observation, molecular genetic visualization of massage responsive CLTMs in mice revealed a denser distribution in dorsal than ventral thoracic sites, greater proximal than distal limb innervation and a complete absence from glabrous paw skin [12]. This latter finding is also supported by human microneurography studies as CTs, while encountered as frequently as other C-fibres in the hairy skin of the body, have not been found on the glabrous skin of the palm or soles of the feet [13]. While the wider anatomical distribution of CTs in human skin is not known, psychophysical studies have reported variation in the perceived pleasantness of CT activating touch across skin sites [14–16].

Attesting to the social importance of touch, mirror neuron type responses to observed touch have been reported, with the same neural regions showing activation as when the touch is experienced first-hand [17]. Furthermore, Morrison et al. [18] reported vicarious responses to dynamic stroking touch are velocity tuned and socially specific, with significantly greater activation seen in posterior insula cortex to CT optimal velocity social stroking than to non-CT optimal velocities or to non-social dynamic touch. Individual differences in vicarious responses to touch have been reported, differing for example on the basis of personality traits or cognitive state [19,20]. In support of a close connection between tactile experience and vicarious responding, patients carrying a heritable mutation which leads to reduced C-fibre density not only rate directly experienced CT optimal touch as less pleasant [21] but are also less sensitive to the rewarding value of observing the same touch than controls. Anatomically, their flattened ratings are associated with reduced activation within posterior insula cortex in response to the observed actions [22].

In the present study we examined whether affective responses to observed social touch reflect the predicted anatomical distribution and known velocity tuning of CTs. We hypothesized we would see the same velocity dependent psychophysical response curves in ratings of observed touch delivered on CT innervated hairy skin sites as have been reported to felt touch, but no such CT optimal velocity tuned profile would be observed in response to touch on glabrous skin. Furthermore, we anticipated that ratings would be anatomically dependent, with higher ratings proximally where CT innervation, based on rodent studies, is hypothesized to be most dense.

2. Methods

2.1. Participants

A total of 84 participants (Mean age 21.21 +/−1.79, 52 women) took part in this study online via the Flash-based Xperiment software package: http://www.xperiment.mobi. Most of the participants were students who took part in exchange for course credit. The study was approved by the LJMU Psychology Research Ethics Committee.

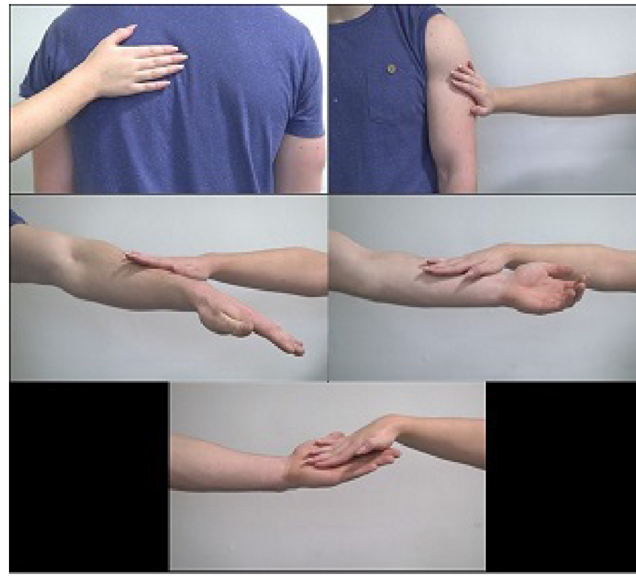

Fig. 1. Stills from the videos presented, one depicting each of the 5 locations studied. The clips lacked any social context, faces were not visible, and showed only the hand and forearm of one female actor "the toucher" and the relevant upper body part (back, arm or palm) of the other male actor "the receiver.".

2.2. Materials & methods

Participants viewed and rated a random sequence of 15 short (5 s) videos depicting one individual being touched by another at 5 different skin sites (back, upper arm, ventral forearm, dorsal forearm and palm) and at 3 different velocities (static, 3 cm/s, 30 cm/s). (Fig. 1 shows video stills, depicting the 5 body sites investigated). Immediately after viewing each clip a new screen appeared where participants were asked to rate, on a Likert scale: (1) *How pleasant do you think that action was for the person being touched?*: (2) *How much would you like to be touched like that?:* 1 not at all – 7 extremely. These two questions always appeared in the same order, each on a new screen, with question 2 appearing directly after the response to question 1 was made. They were designed to probe expectations of how touch is perceived by others versus self.

2.3. Statistical analysis

Following the method described by Tabachnik and Fidell [2013], one multivariate outlier was identified and excluded from further analysis. Briefly this involved calculating one Mahalanobis value per participant, taking into account their model residuals for each of the 30 conditions and using the critical chi square (59.703 for 30 predictors and $p < 0.001$) as the cut-off value. For all conditions, model residuals had skewness and kurtosis z-scores <3.29 indicating data fit a normal distribution. Multivariate statistics with Pillai's Trace *F* estimation are reported. Sidak correction was applied to comparisons of significant main effects where appropriate. A repeated measures ANOVA with within subject factors of question (2 levels), location (5 levels) and velocity (3 levels) was conducted. A significant Question x Location x Velocity interaction was identified ($F_{8,75} = 2.298$, $p = 0.029$, $\eta_p^2 = 0.197$, power = 0.846), so each question was analysed separately.

MLwiN was used to carry out regression analyses on the two questions separately, to determine whether a quadratic expression described significantly more of the variance than a linear expression alone. Multi-level modelling was used and random factors of participant and trial number were included in the model with a fixed factor (predictor) of velocity. The outcome variable was rating. This was carried out for each location individually as well as com-

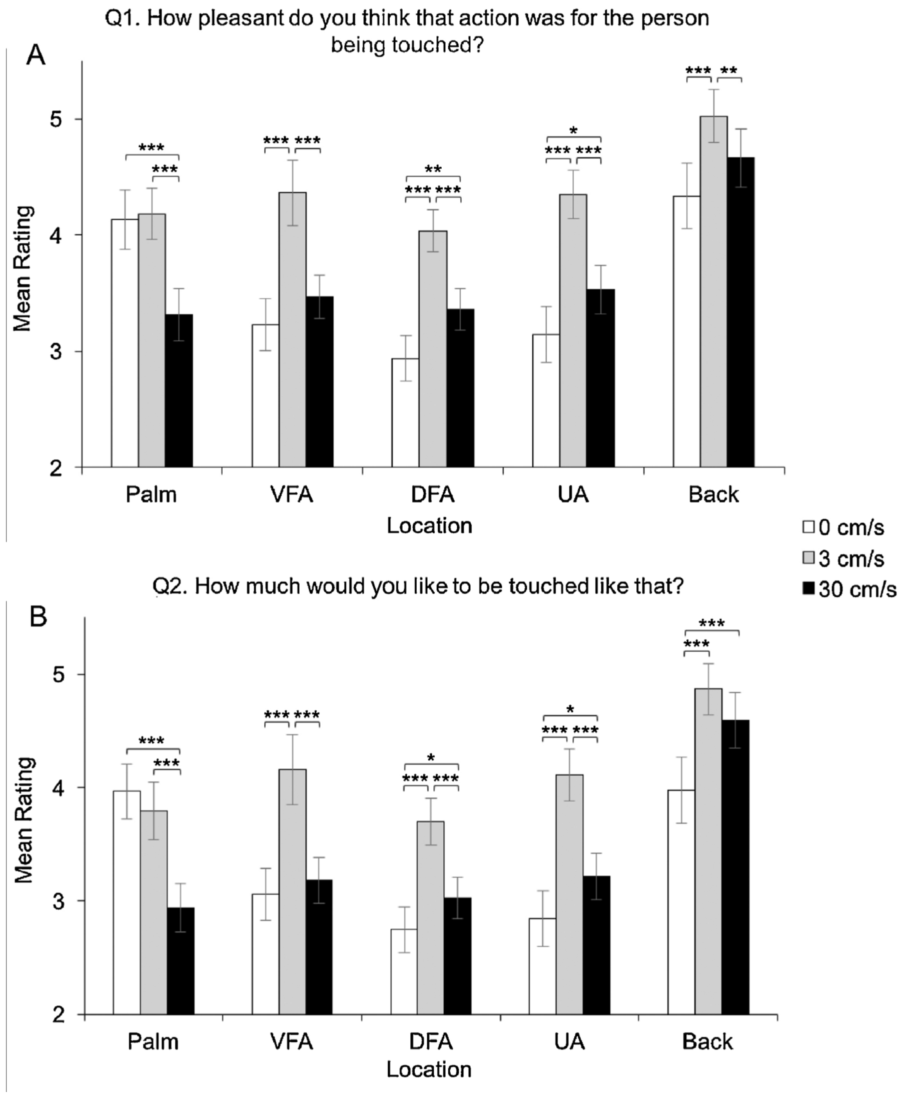

Fig. 2. A. Mean Pleasantness Ratings (+/− 95% CI) for touch at each of 5 skin sites across the 3 stroking velocities for question 1. B. Mean Pleasantness Ratings (+/− 95% CI) for touch at each of 5 skin sites across the 3 stroking velocities for question 2. For both questions there is a significant main effect of velocity and of location as well as a significant touch x velocity interaction. The CT optimal velocity of 3 cm/s was rated significantly more positively than CT non-optimal velocities of 0 and 30 cm/s when touch was applied to the ventral (VFA) and dorsal forearm (DFA), and the upper arm (UA) (all p's <0.001). For touch to the palm, 30 cm/s was rated significantly more negatively than static and 3 cm/s touch (all p's <0.001). In question 1, touch to the back at 3 cm/s was rated significantly more pleasantly than either static ($p<0.001$) or 30 cm/s touch ($p<0.05$). In question 2, touch to the back at 3 cm/s was rated significantly more positively than static touch ($p<0.001$).

paring the effect of velocity of all hairy skin locations to the palm. Model residuals were examined using Q-Q plots and histograms to verify the assumption of normality was met. The outlier identified and excluded from the ANOVA analysis was also excluded from these analyses.

3. Results

Q1. How pleasant do you think that action was for the person being touched?

A significant main effect of velocity was identified ($F_{2,81}=46.242$, $p<0.001$, $\eta_p{}^2=0.533$, power = 1.000), with 3 cm/s being rated significantly more positively than the other two velocities (all p's <0.001). There was also a significant main effect of location ($F_{4,79}=24.279$, $p<0.001$, $\eta_p{}^2=0.551$, power = 1.000), with touch on the back being rated significantly higher (all p's <0.001) than any other location. There was a significant touch x velocity interaction ($F_{8,75}=7.051$, $p<0.001$, $\eta_p{}^2=0.429$, power = 1.000) which reflected the fact that CT optimal (3 cm/s) touch was significantly preferred to static touch at all skin sites (all p's <0.001) except the palm of the hand, consistent with the absence of CTs in glabrous skin. 3 cm/s stroking was significantly preferred to 30 cm/s at all 5 locations (all p's <0.005). (See Fig. 2A).

Q2. How much would you like to be touched like that?

For this question too, a significant main effect of velocity was identified ($F_{2,81}=40.419$, $p<0.001$, $\eta_p{}^2=0.499$, power = 1.000), with 3 cm/s being rated significantly more positively than the other two velocities (all p's <0.001). There was also a significant main effect of location ($F_{4,79}=28.464$, $p<0.001$, $\eta_p{}^2=0.590$, power = 1.000), with touch on the back being rated significantly higher (all p's <0.001), than any other location. Again, there was a significant touch x velocity interaction ($F_{8,75}=10.893$, $p<0.001$, $\eta_p{}^2=0.537$, power = 1.000) which reflects the fact that, in contrast to all other skin sites, CT optimal (3 cm/s) touch on the palm of the hand was not preferred to static touch, consistent with the absence of CTs in glabrous skin. Also, 3 cm/s stroking was significantly pre-

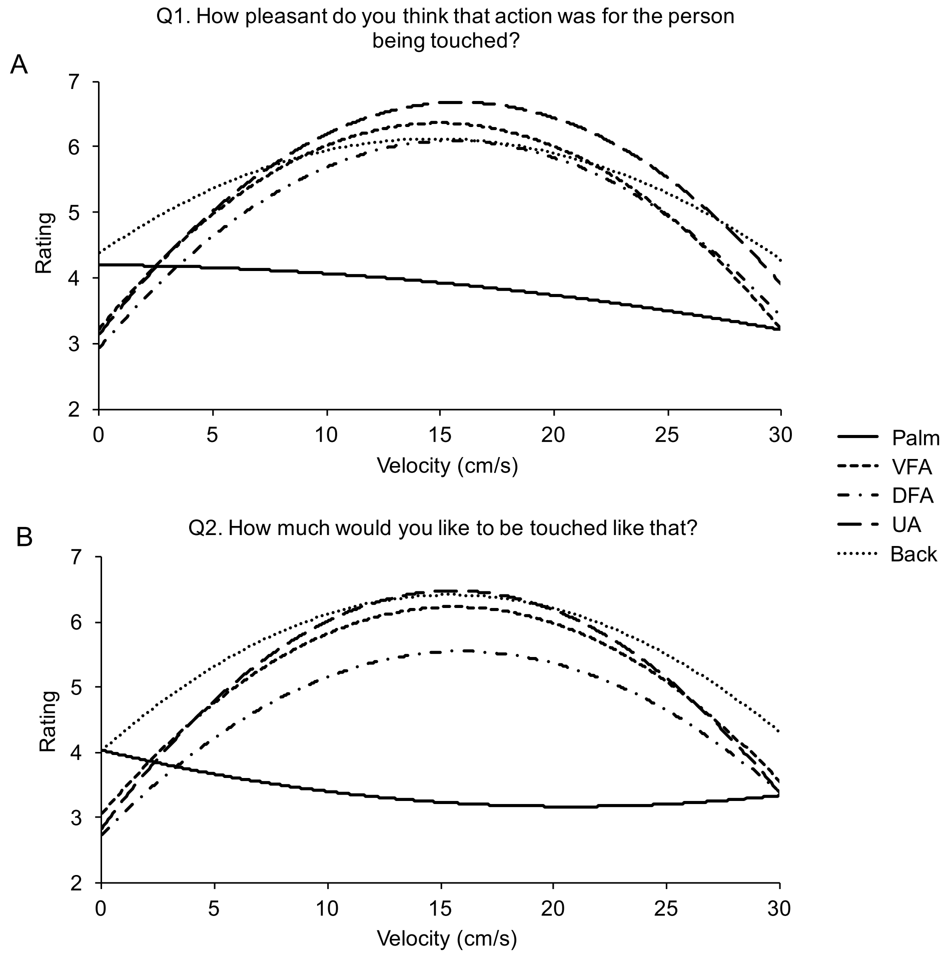

Fig. 3. A. Regression curve for ratings of touch at each of the 5 skin sites for question 1. B. Regression curve for ratings of touch at each of the 5 skin sites for question 2. In both questions for touch applied to CT innervated hairy skin sites, i.e. the back, upper arm (UA) dorsal forearm (DFA) and ventral forearm (VFA), a quadratic regression term explained significantly more of the variance than a linear regression term (all p's < 0.001). However, for the glabrous skin of the palm neither a quadratic nor linear term provided a significant fit for the data.

ferred to 30 cm/s at all locations (all p's < 0.001) except the back where no significant difference in pleasantness ratings between 3 and 30 cm/s touch was found (t_{82} = 1.924, p_S = 0.162). (See Fig. 2B).

As can be seen by comparing Fig. 2A & B the significant question x location x velocity interaction reflects differences between ratings of touch on the back when considering the self or another. While for question one (other) CT-optimal 3 cm/s touch was rated significantly higher than either static or 30 cm/s, for question 2 (self) CT-optimal touch was only significantly preferred to static, not 30 cm/s. However, a correlation analysis revealed that responses to question 1 & 2 were strongly and significantly correlated (r = 0.901, p < 0.001) suggesting they don't elicit distinct responses. This is further supported by the regression analysis.

3.1. Regression analysis

For both question 1 & 2, at all hairy skin sites, a quadratic regression term explained significantly more of the variance than a linear regression term (all p's < 0.001). However, on the palm of the hand, for question 1 neither the linear (z = −0.053, p = 0.479) nor quadratic (z = −0.5, p = 0.309) term explained a significant proportion of the variance in ratings of touch pleasantness. The same was true for question 2 (linear z = −1.456, p = 0.073; quadratic z = 1.000, p = 0.159.

3.2. Full model

Finally, for both questions, it was determined whether the quadratic terms describing velocity for each CT innervated location were significantly different to those of the palm. In response to both questions at each of the 4 CT innervated locations, the quadratic term was significantly more negative (steeper inverted U) than that of the palm (Q1 $z \leq -2.000$, p < 0.023 & Q2 $z \leq -3.667$, p < 0.001). (See Fig. 3A&B).

4. Discussion

Consistent with our hypothesis, the highest ratings of reported pleasantness were for observing gentle touch delivered at CTs' preferred stroking speed. This finding is in line with previous research showing that seen-touch produces the same subjective and affective responses as felt-touch [18,22] and demonstrates that humans have a preference for CT optimal, caressing touch. By looking at a broader range of skin sites and stroking velocities, we extend the findings of previous research, showing that the psychophysical curves from our vicarious rating task are consistent with the findings from previous microneurography studies and psychophysical assessments [4,16]. That is, at all CT innervated (hairy) skin sites a negative quadratic function provided the best fit for describing the relationship between perceptions of touch pleasantness and

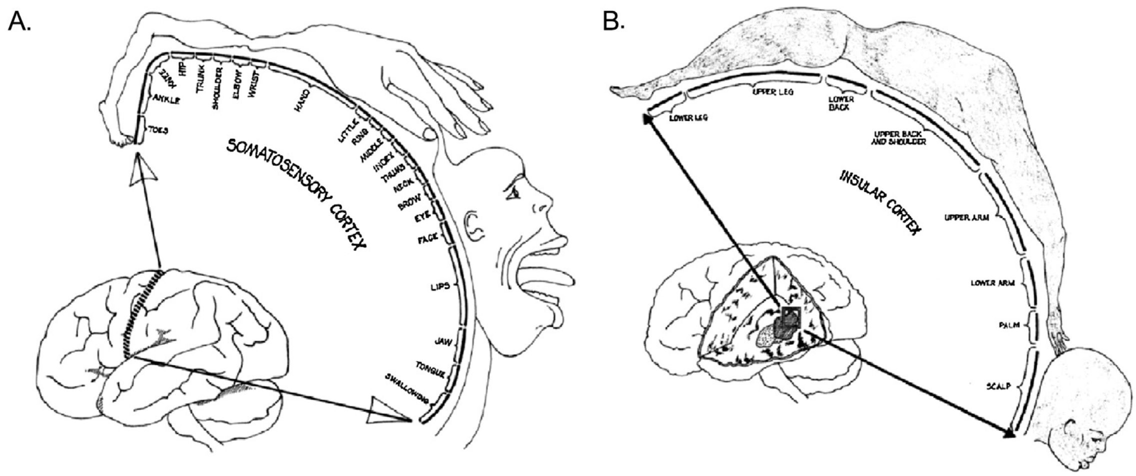

Fig. 4. A. Penfield's iconic sensory homunculus depicts the representation of discriminative touch in somatosensory cortex. The amount of cortex devoted to a body part is proportional to the relative density of cutaneous tactile receptors in that region. B. The results of the present study, along with the known somatotopic organisation in the processing of affective tactile stimuli, suggest a hedonic homunculus may exist to be mapped, within insula cortex, reflecting the relative innervation density of CTs across the body.

stroking velocity. However, on the palm of the hand neither a linear nor quadratic function described the data. Of the body sites we examined, touch on the back was rated as most pleasant. Such preferences match the specific anatomical distribution of CLTMs, mapped in mice [12] and the apparent enhanced rewarding value, indicated by larger evoked dopamine release in the NAC, to dynamic touch on the back versus the limbs [11]. Thus, taken together our results indicate that people recognise that the most pleasant touch occurs in locations where CTs are abundant, at speeds which activated them most strongly.

Perceptions of touch are typically context dependent; how pleasant a given tactile interaction is reported to be varies both with who is doing the touching and where on the body the touch occurs [23]. In this study we have been careful to exclude all social context from the clips shown and the touch occurs only at body sites where people rate touch positively in a range of social contexts [24]. It remains to be systematically tested how contextual features of a social interaction specifically influence perceptions of CT activating touch.

While we didn't see clear differences in the way participants responded to the self versus other focused questions we used in the present study they are likely to prove useful in future studies probing how an individual's state or trait experience of touch impacts their vicarious ratings [25]. For example, to date a number of studies have reported that neural responses to both experienced and seen touch vary in relation to several personality traits [19,26]. A recent fMRI study reported blunted neural responses to affective touch in children and adolescents with autism spectrum disorder (ASD), in comparison to typically developing controls [27]. Given that individuals with ASD frequently show atypical behavioural responses to both social and tactile stimuli it would be of interest to examine whether their ratings of our affective touch videos show the typical psychophysical relationships between location, velocity and liking.

Penfield's iconic sensory homunculus depicts the representation of discriminative touch in primary somatosensory cortex (S1), with the amount of cortex devoted to a body part being proportional to the relative density of cutaneous tactile receptors in that region of the body (Fig. 4A). Indeed vicariously experienced touch has previously been reported to activate S1 in the same somatatopically organised manner as felt touch – reflecting the classic homunculus [28]. fMRI studies have demonstrated an anatomical dissociation of discriminative (Aβ mediated) from emotional (C-fibre mediated) neural representations of touch [29], with unmyelinated tactile afferents projecting to posterior insular cortex [30]. Somatotopic organisation within the posterior insula has been reported in the processing of both painful and gentle tactile stimuli [31–33]. Thus, taken together with the findings from the present study, this suggests a second, affective or "hedonic homunculus" may exist, perhaps within insula cortex, reflecting the relative innervation density of CTs across the body (Fig. 4B). Future studies are needed to address this question.

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