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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.

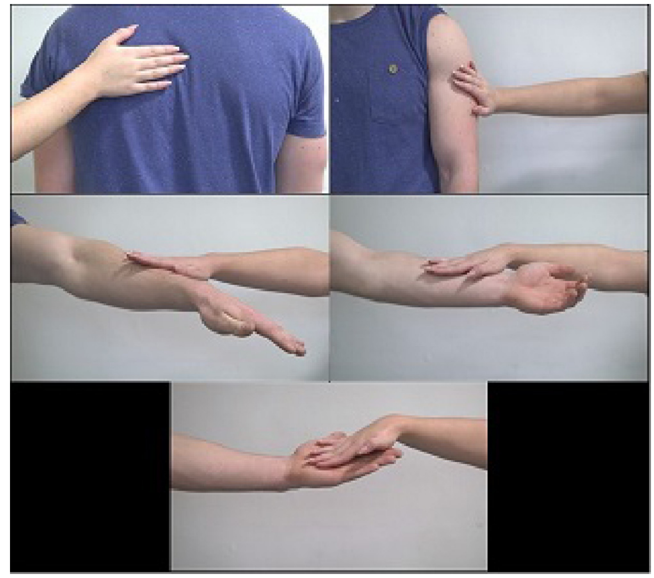

Fig. 1. Stills from the videos presented, one depicting each of the 5 locations studied. The clips lacked any social context, faces were not visible, and showed only the hand and forearm of one female actor "the toucher" and the relevant upper body part (back, arm or palm) of the other male actor "the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