

RESEARCH ARTICLE

Children's vicarious ratings of social touch are tuned to the velocity but not the location of a caress

Connor J. Haggarty¹ , Paula D. Trotter¹, Francis McGlone^{1,2}, Susannah C. Walker^{1*} 

1 Research Centre for Brain & Behaviour, School of Psychology, Liverpool John Moores University, Liverpool, United Kingdom, **2** Institute of Psychology, Health & Society, University of Liverpool, Liverpool, United Kingdom

✉ Current address: Centre for Social and Affective Neuroscience, Linköping University, Linköping, Sweden
* S.C.Walker@ljmu.ac.uk



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Abstract

Affective sharing is a bottom-up process involving automatic processing of sensory inputs that facilitate vicarious experience of another's emotional state. It is grounded directly in the prior experiences of the perceiver. In adults, vicarious ratings of affective touch match the known velocity tuning and hypothesised anatomical distribution of C-tactile afferents (CT), a subclass of C-fibre which respond preferentially to low force/velocity stroking touch, typically perceived as pleasant. Given the centrality of touch to early nurturing interactions, here we examined whether primary school aged children's vicarious ratings of affective touch show the same anatomical and velocity specific patterns reported in adults. Forty-four children aged between 8 and 11 (mean age 9, 24 male) rated a sequence of video clips depicting one individual being touched by another on 5 different upper-body sites (palm, dorsal forearm, ventral forearm, upper-arm and back) at 3 different velocities (static, CT optimal, slow stroking and non-CT optimal, fast stroking). Immediately after viewing each clip, participants were asked to rate how pleasant they perceived the touch to be. While children rated the CT optimal velocity significantly higher than static or non-CT optimal touch, unlike adults their ratings did not vary across skin sites. This difference may reflect the fact children's ratings are grounded in bottom-up affective resonance while adults also draw on top-down cognitive evaluation of the broader social context when rating the stimuli.

1. Introduction

Affective resonance is a bottom-up process which involves automatic processing of sensory inputs that facilitate vicarious experience of another's emotional state [1]. The neural basis of affective sharing has been widely studied using pain observation paradigms, which reveal significant overlap between brain areas activated during vicarious and first-hand experience of pain [2–4]. Affective resonance for pain can be observed whether an actor's facial expressions are being observed or not [4–6]. For example, viewing body parts in a painful condition in the absence of a broader social context results in common activation of brain regions as

self-experienced pain [6]. The perception-action coupling mechanisms which underpin affect sharing are present implicitly from birth [7, 8] and become explicit with experience through childhood and adolescence [9, 10]. They are thus likely to provide the initial mechanism upon which, higher order, top-down processes required for cognitive empathy are built [1].

Just as with pain, people show affective empathy for vicariously experienced touch [11–14]. For example, viewing another person receive social, caressing touch elicits the same velocity dependent responses in the posterior insula cortex as are reported when the same stimulus is experienced first-hand [14]. These findings suggest that the velocity of touch is a key feature which people use to determine its affective content. Indeed, there is neurobiological support for this hypothesis; a class of unmyelinated c-fibres has been identified and characterised in the hairy skin of mammals that are tuned to exactly the stimulus velocities which, in psychophysical studies, participants perceive as most pleasant [15–17]. That is, single unit microneurography recordings show these c-tactile afferents (CTs) fire most prominently to a stimulus moving across their receptive field at 1–10cm/s, the very velocity range which reliably produces the highest hedonic ratings when participants experience gentle stroking touch [16].

Evidence that affect sharing is grounded directly in the prior experiences of the perceiver comes from study of patients carrying a heritable mutation which leads to reduced c-fibre density [18]. In addition to blunted temperature and pain sensitivity, patients with this hereditary sensory and autonomic neuropathy type V (HSAN-V) mutation do not report velocity dependent ratings of gentle, moving touch and furthermore, show exactly the same flattened pattern of ratings to vicariously experienced touch. Neurally, whether experiencing touch first-hand or vicariously, HSAN-V patients' responses within posterior insular cortex showed no distinction between stimuli moving at a CT optimal 3cm/s or a non-CT optimal 30cm/s. Overall, despite reporting the same levels of interpersonal touch as the control group, HSAN-V patients haven't learned that stimulus velocity is an important cue for judging its affective value [18]. These data provide important evidence both that vicarious ratings are grounded in the viewer's own perceptual experience and that CTs contribute to the development of pleasant touch perception. Further indication that personal experience shapes affective touch ratings comes from a recent psychophysical study where young adults, who as children experienced abuse and or neglect, showed blunted sensitivity to CT-targeted touch, whether experienced first-hand or vicariously. Again, this was despite the fact they reported the same levels of current intimate social touch as the control group [19].

The notion that early social tactile experience shapes adult perceptions of affective touch is not surprising given the centrality of touch to early nurturing interactions and its role in promoting attachment formation [20–22 for reviews]. Indeed, neuroimaging data shows that the CT system is functional from birth [23, 24] and parents spontaneously caress their infant at CT optimal velocities [25–27]. While neural differentiation between discriminative and affective aspects of touch develops over the first 12 months of life [28–31], behaviourally, by 9 months of age, children show an attentional bias to CT-targeted over faster or slower skin stroking [32]. Indeed, once old enough to use a rating scale, in a psychophysical study young children showed similar, velocity dependent ratings of affective touch as adults [33].

In addition to velocity, another cue to the affective value of social touch is location. While the anatomical distribution of CTs in human skin is not known, psychophysical studies have reported variation in the perceived pleasantness of CT-targeted touch across skin sites [15, 34, 35] and biopsy studies reported higher density of epidermal c-fibres on the back than proximal limb sites [36]. This is consistent with molecular genetic visualization of massage responsive C-low threshold mechanoreceptors (CLTMs—the presumed rodent homologue of CTs) in mice which revealed a denser distribution in dorsal than ventral thoracic sites, greater proximal than distal limb innervation and a complete absence from glabrous paw skin [37]. Though

velocity tuning of rodent CLTMs has not been established, stroking touch applied to rats at CT optimal velocities elicits dopamine release within the nucleus accumbens (NAC). The effect is anatomically specific, as stroking applied to the back elicited a significantly greater dopamine response than stroking the limbs or abdomen [38]. Consistent with this report, several behavioural studies, in humans and animals, have established that selective CLTM activation, or application of touch which should optimally activate CTs, is motivating and its rewarding value is learned rapidly [39–42].

We have previously reported that adults' affective responses to observed social touch reflect the predicted anatomical distribution and known velocity tuning of CTs [19, 43]. That is, we observed 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. Furthermore, people rated touch on the back, where CT innervation is hypothesized to be most dense, higher than on more proximal sites. While, in psychophysical tests using directly felt touch, the same velocity dependent relationship between pleasantness and touch has been reported on the palm as on the arm [44], we did not see the equivalent velocity tuned profile in response to observed touch to the palm [19, 43]. This difference may reflect the fact our stimuli included a static touch condition, which while being highly relevant to many social tactile interactions, such as hand holding, is not generally studied psychophysically, where dynamic stroking is typically used.

The aim of the present study was to determine whether children's ratings of vicariously experienced affective touch show the same velocity and anatomical specificity as adult ratings. We hypothesised, given the centrality of touch to nurturing interactions and early behavioural sensitivity to the specific rewarding value of CT targeted touch, that such preferences would be observable early in development and so children's rating patterns would match those previously reported in adults.

2. Methods

2.1 Participants

Forty-four children aged 8–11 years (mean 9 years \pm 0.9, 24 male), were recruited from years 4, 5 and 6 of a primary school in the Northwest of England. Parents/Guardians gave written informed consent for their child's participation. Each child also provided informed assent before beginning the study. The study was approved by the LJMU Psychology Research Ethics Committee.

2.2 Materials & methods

Participants viewed and rated a random sequence of 15 short (5 sec) videos depicting one male individual being touched by a female at 5 different skin sites (back, upper arm, ventral forearm, dorsal forearm and palm) and at 3 different velocities (Static touch, slow—CT optimal strokes and fast—non-CT optimal strokes). (Fig 1A shows video stills, depicting the 5 body sites investigated) [43]. Immediately after viewing each clip, a new screen appeared where participants were asked make a hedonic rating using a smiley face scale (designed and validated for use with young children by Cascio et al & Croy et al [33, 45]—see Fig 1B): (1) Thinking about the video you have just watched answer the question below by choosing a face. How nice do you think it was for the person being touched? (2) Again, thinking about the same video answer the question below by choosing a face. How much would you like to be touched like that? 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.

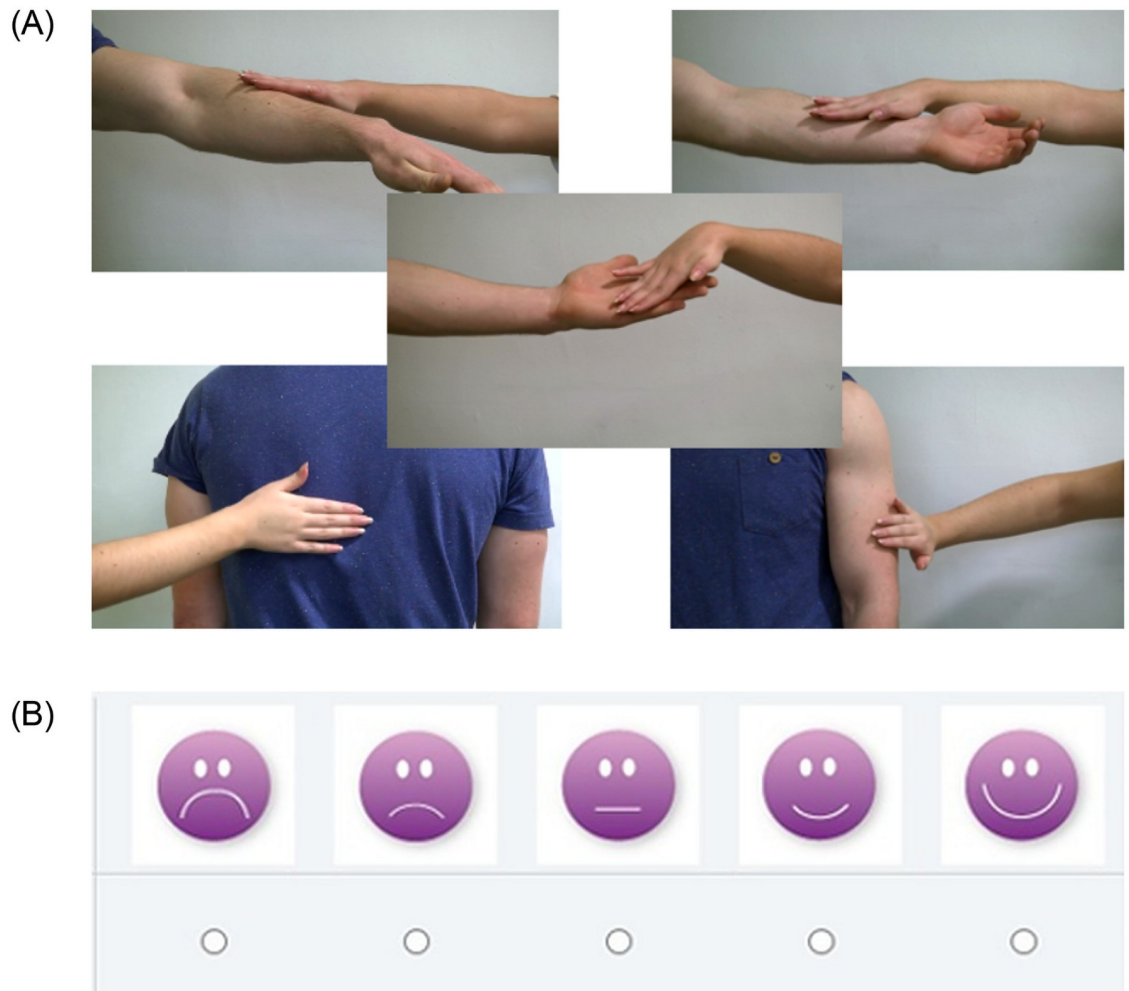


Fig 1. (A) Stills from the videos presented, one depicting each of the 5 locations studied. The clips lacked any social context, faces were not visible, and showed only the hand and forearm of one female actor “the toucher” and the relevant upper body part (back, arm or palm) or the other male actor “the receiver.” (B) Example of the smiley face scale used for measuring the children’s affective touch ratings. (adapted from 35,47).

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2.3 Procedure

Children completed the experiment in a computer classroom at school. All testing took place on the same morning and was conducted in 4 sessions with 8–13 children present in each. Initially, the experimenter read through a short information sheet with the group and before beginning, children were asked if they still wished to take part. To prevent students being influenced by their peers they were asked to sit at computers with an empty space between each other. The experimenter then gave a brief overview of what they were going to do. To test their understanding of how to use the rating scale, initially several images of different types of food were displayed on a projector screen at the front of the room. Children were instructed to use the smiley face scale to rate the different types of food. The food shown included a variety of items that the children were likely to really like, items they were likely to rate neutrally and finally items they were likely to dislike (Images included, chocolates and French fries, carrots, beans, strawberries and apples, sprouts and mushrooms). Each type of food was displayed one at a time in a random order. Once it was clear to the experimenter that all the children

understood how to use the scale, further instructions were given. Children were told that in a few moments, they would view a series of videos each showing a person being touched. It was made clear that two questions would appear following each video, which they were required to answer honestly as there were no right or wrong answers. Before the first video was shown, children were required to enter their age. If the students had no further questions, they were instructed to begin. The children watched each video at their own computer, allowing them to work through the questions at their own pace. After all the children had finished, they were fully debriefed and returned to their classes. The study was hosted in Qualtrics version 04 2018 (Provo, UT) survey software.

2.4 Statistical analysis

Following the procedure of Croy et al [33], in their previous use of this rating scale to measure children's perception of affective touch, the ratings from the pictorial scales were converted into numbers (1-very bad, 2-bad, 3-neutral, 4-happy, 5-very happy). Subsequently, data were analyzed in SPSS (Version 26) using a generalized linear model with ordinal logistic link function; Velocity (3 levels) and Location (5 levels) were entered as within subject factors, subject was entered as a random factor. Significant main effects were followed up using Wilcoxon Signed Ranks tests for non-parametric data. Due to a coding error, it is not possible to match up a participant's gender to their age and touch rating data. Figures were drawn using R packages tidyverse and ggsignif.

3. Results

Q1. How nice do you think it was for the person being touched?

A significant main effect of velocity was identified (Wald $\chi^2(2) = 34.11, p < 0.001$), with Wilcoxon Signed Ranks tests confirming CT optimal (~3cm/s) touch was rated significantly more positively than the other two velocities ($ps < 0.002$). While there was a trend for static touch to be rated less positively than fast (~30cm/s) touch, this did not reach the threshold for significance ($p = 0.06$). There was no significant main effect of location (Wald $\chi^2(4) = 2.33, p = 0.68$), nor was there a significant location by velocity interaction (Wald $\chi^2(8) = 14.28, p = 0.08$). See Fig 2.

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

For this question too, a significant main effect of velocity was identified (Wald $\chi^2(2) = 30.96, p < 0.001$) with Wilcoxon Signed Ranks tests again confirming CT optimal (~3cm/s) touch was rated significantly more positively than the other two velocities ($ps < 0.002$). Ratings of static and fast (~30cm/s) touch did not differ significantly ($p = 0.14$). For this question too, there was no significant of location (Wald $\chi^2(4) = 7.72, p = 0.10$), nor was there as significant location by velocity interaction (Wald $\chi^2(8) = 12.95, p = 0.11$). See Fig 3.

Thus, whether considering self or other, while children, like adults, rated the CT optimal (~3cm/s) touch as significantly more pleasant than either static or fast (~30cm/s) touch, their ratings did not vary across body sites.

Relationship between responses to question 1 and 2

Spearman's correlations confirmed that, as previously reported with adults [43], responses to the self and other questions were significantly correlated (static $r_s = .34, p = 0.01$, CT $r_s = .55, p < .001$, non-CT $r_s = .57, p < .001$).

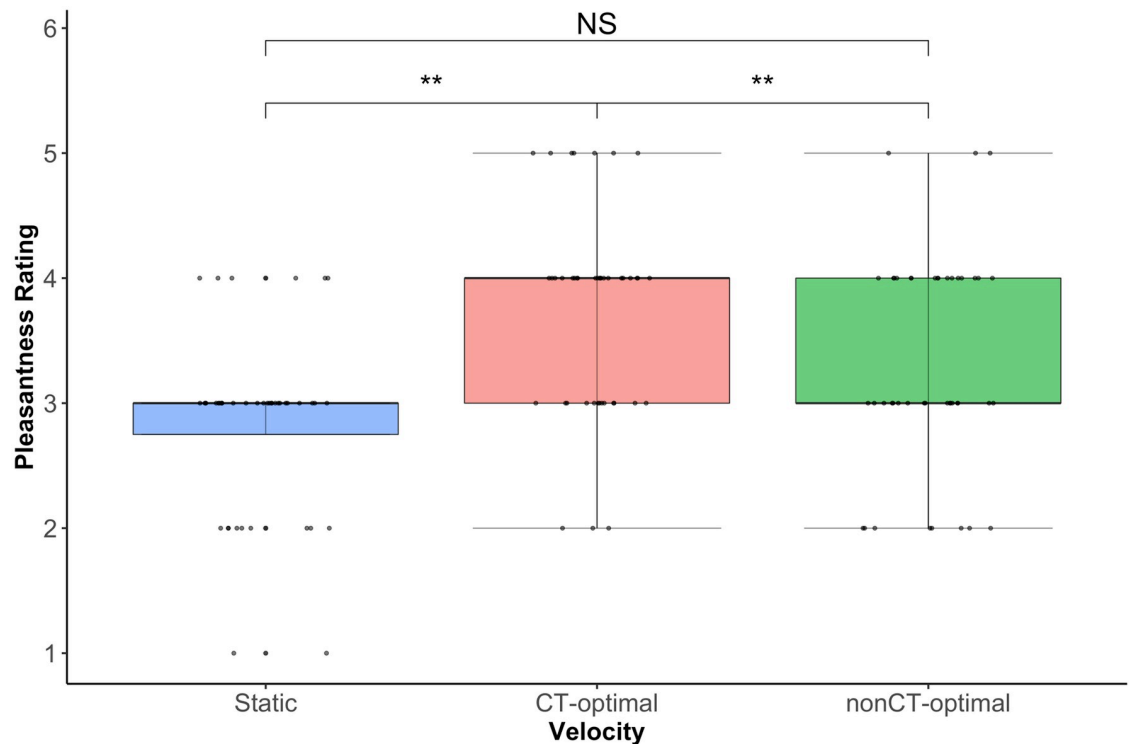


Fig 2. Box and whisker plot showing median pleasantness ratings (thick black line) for touch at the 3 stroking velocities for question 1. Dots represent individual participant ratings. There is a significant main effect of velocity ($p < 0.001$), but no effect of location, or location \times velocity interaction. Wilcoxon Signed Ranks tests confirmed that the CT optimal velocity, slow stroking touch was rated significantly more positively than either static or fast stroking, non-CT optimal velocity touch, $**p < 0.002$.

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4. Discussion

Consistent with our hypothesis, primary school age children rated the vicarious observation of slowly moving touch, optimal for activating CTs, as significantly more pleasant than static or faster, non-CT optimal touch. This finding is in line with previous studies in adults showing that seen-touch produces the same, velocity dependent affective responses as felt-touch [14, 18, 19, 43]. However, contrary to our prediction, children's rating patterns do not vary according to the skin site being touched. This contrasts with two previous studies using these same video stimuli with adults, where touch on the back was rated higher than touch on more proximal arm and palm sites [19, 43]. Furthermore, unlike adults, children's ratings of touch to the glabrous skin of the palm showed the same relationship between velocity and perceived pleasantness as on the other, hairy skin sites shown. In contrast, we have previously found that adults rate vicariously experienced, static touch on the palm equally pleasant to CT-optimal touch [19, 43]. Taken together, these findings show that, as with adults, children use velocity as a cue to determine the affective value of social touch. This is consistent with psychophysical, behavioral and neuroimaging studies showing the CT system is functional from birth and that children differentiate the affective qualities of CT optimal and non-CT optimal touch [23, 24, 32, 33]. This is also consistent with studies of vicarious pain which report affective resonance to dynamic depictions of painful touch, which, like our stimuli, lacked a broader social context [46].

The lack of topographical differentiation in the children's ratings could be explained by several factors. On the one hand, children may not yet have had sufficient touch exposure and

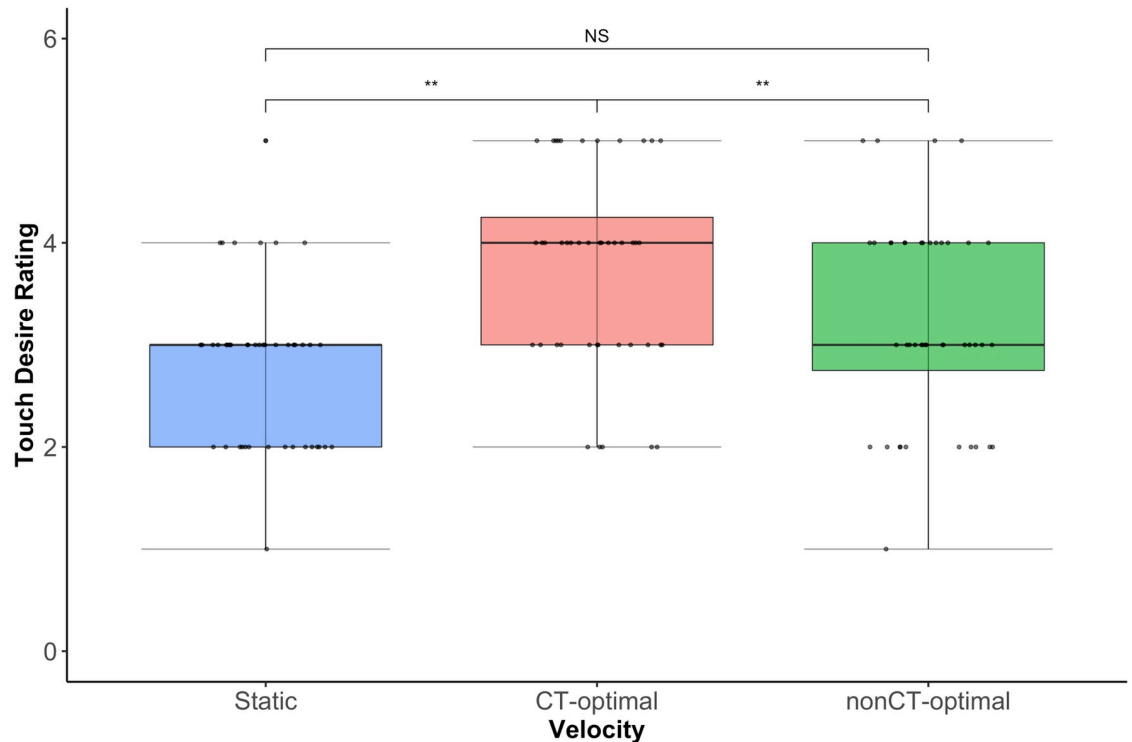


Fig 3. Box and whisker plot showing median pleasantness ratings (thick black line) for touch at the 3 stroking velocities for question 2. Dots represent individual participant ratings. As per question 1, there is a significant main effect of velocity ($p < 0.001$), but no effect of location, or location \times velocity interaction. Wilcoxon Signed Ranks tests confirmed that the CT optimal velocity, slow stroking touch was rated significantly more positively than either static or non-CT optimal velocity touch, $**p < 0.002$.

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experience to differentiate affective values across skin sites. That could be because static touch to the palm, a hand on the shoulder, or a back rub are more typical of adult-to-adult interactions than the adult-child or child-child interactions, which the children are presumably drawing on to make their affective responses. 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 [47]. Our stimuli excluded 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 [47, 48]. However, it could be that the topographical differentiations shown in adult ratings rely on top-down cognitive processes, drawing on a context which isn't explicitly provided in the videos, while children's ratings reflect a purely bottom-up affective resonance. If that is the case, it remains to be determined whether this difference is experience dependent or whether children lack the top-down cognitive empathic abilities necessary for the previously reported anatomical distinctions to emerge [9]. Future work could systematically test how contextual features, such as the age and gender of the actors in the social interaction, influence affective ratings. Alternatively, the inherently limited variance produced with the child-friendly rating scale we used here may have meant we lacked the sensitivity to differentiate between skin sites [45]. However, we think this is unlikely as in adults we only used a 7-point Likert scale and here children's ratings did vary by velocity and were not at ceiling or floor for any clip presented.

Here, as with our previous study, we did not see any difference in the self-versus other focused questions we posed. This is consistent with previous studies with patient's lacking c-fibres, whose vicarious ratings of moving touch mapped directly on to their ratings of directly

experienced touch, providing strong evidence that affective resonance is indeed grounded in the viewer's own perceptual experience [18]. It is also important to note that while here we would not necessarily expect the children's experiences to differ strongly from others they know, in future studies the two questions may be useful in probing how trait and state factors modify vicarious ratings. For example, a number of studies have reported that neural responses to both experienced and seen touch vary in relation to several personality traits [49–51]. Furthermore, tactile sensitivities are commonly reported in children and adults with developmental disorders and autism spectrum conditions (ASC) [45, 52]. Indeed, fMRI data reveals blunted neural responses to affective touch in children and adolescents with ASC, in comparison to typically developing controls [53]. Thus, it would be interesting to determine whether these groups recognize that their affective tactile experiences are atypical to those of family and friends. A limitation of our study design may be that our self and other questions directly follow each other, which could prime participants to simply enter the same response again. We chose this design to try to avoid participants getting confused by the question they are answering at a given point. However, in future perhaps a blocked design, where participants rate all of the videos twice, once in relation to themselves and once in relation to a specific other, in a counterbalanced order, may improve sensitivity of this measure.

Given somatotopic organization within the posterior insula has been reported in the processing of both painful and pleasant tactile stimuli [54–56], we have previously proposed that the anatomical differentiation of adult's vicariously experienced affective touch ratings reflect the hypothesized anatomical distribution of CTs [43]. However, given the absence of this differentiation in the current study, perhaps they rather reflect adult's top-down, cognitive evaluation of the video stimuli. Future studies using fMRI may facilitate the testing of these alternative possibilities. While responses in posterior insula cortex to dynamic social, but not nonsocial, touch vary according to velocity [14, 18], activity here does not correlate with participant ratings of touch pleasantness. However, responses in posterior superior temporal sulcus and orbitofrontal cortex have previously been found to correlate with the subjective value of sensory stimuli, including affective touch [57–59]. Furthermore, activity in primary somatosensory, but not posterior insula, cortex has been found to vary according to the visual context in which a caress is experienced [60]. Thus, determining where in the brain these anatomically differentiated vicarious touch ratings are represented would give insight into the underlying sensory and cognitive processes.

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Author Contributions

Conceptualization: Connor J. Haggarty, Paula D. Trotter, Francis McGlone, Susannah C. Walker.

Formal analysis: Susannah C. Walker.

Funding acquisition: Francis McGlone, Susannah C. Walker.

Methodology: Connor J. Haggarty, Paula D. Trotter, Francis McGlone, Susannah C. Walker.

Supervision: Susannah C. Walker.

Visualization: Connor J. Haggarty.

Writing – original draft: Susannah C. Walker.

Writing – review & editing: Connor J. Haggarty, Paula D. Trotter, Francis McGlone, Susanah C. Walker.

References

1. Decety J, Meyer M. From emotion resonance to empathic understanding: A social developmental neuroscience account. *Dev Psychopathol.* 2008; 20: 1053–1080. <https://doi.org/10.1017/S0954579408000503> PMID: 18838031
2. Jackson PL, Rainville P, Decety J. To what extent do we share the pain of others? Insight from the neural bases of pain empathy. *Pain.* 2006; pp. 5–9. <https://doi.org/10.1016/j.pain.2006.09.013> PMID: 16997470
3. Morrison I, Tipper SP, Fenton-Adams WL, Bach P. 'Feeling' others' painful actions: The sensorimotor integration of pain and action information. *Hum Brain Mapp.* 2013; 34: 1982–1998. <https://doi.org/10.1002/hbm.22040> PMID: 22451259
4. Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD. Empathy for Pain Involves the Affective but not Sensory Components of Pain. *Science (80-).* 2004; 303: 1157–1162. <https://doi.org/10.1126/science.1093535> PMID: 14976305
5. Botvinick M, Jha AP, Bylsma LM, Fabian SA, Solomon PE, Prkachin KM. Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage.* 2005; 25: 312–319. <https://doi.org/10.1016/j.neuroimage.2004.11.043> PMID: 15734365
6. Jackson PL, Meltzoff AN, Decety J. How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage.* 2005; 24: 771–779. <https://doi.org/10.1016/j.neuroimage.2004.09.006> PMID: 15652312
7. Decety J. The neurodevelopment of empathy in humans. *Dev Neurosci.* 2010; 32: 257–267. <https://doi.org/10.1159/000317771> PMID: 20805682
8. Nielsen L. The simulation of emotion experience: On the emotional foundations of theory of mind. *Phenomenol Cogn Sci.* 2002; 3: 255–286. <https://doi.org/10.1023/A:1021359916894>
9. Decety J, Michalska KJ. Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Dev Sci.* 2010; 13: 886–899. <https://doi.org/10.1111/j.1467-7687.2009.00940.x> PMID: 20977559
10. Lepage JF, Théoret H. The mirror neuron system: Grasping others' actions from birth?: TARGET ARTICLE with COMMENTARIES. *Dev Sci.* 2007; 10: 513–523. <https://doi.org/10.1111/j.1467-7687.2007.00631.x> PMID: 17683336
11. Bolognini N, Rossetti A, Fusaro M, Vallar G, Miniussi C. Sharing social touch in the primary somatosensory cortex. *Curr Biol.* 2014; 24: 1513–1517. <https://doi.org/10.1016/j.cub.2014.05.025> PMID: 24954046
12. Keysers C, Wicker B, Gazzola V, Anton JL, Fogassi L, Gallese V. A touching sight: SII/PV activation during the observation and experience of touch. *Neuron.* 2004; 42: 335–346. [https://doi.org/10.1016/s0896-6273\(04\)00156-4](https://doi.org/10.1016/s0896-6273(04)00156-4) PMID: 15091347
13. Keysers C, Kaas JH, Gazzola V. Somatosensation in social perception. *Nature Reviews Neuroscience.* *Nat Rev Neurosci.* 2010; pp. 417–428. <https://doi.org/10.1038/nrn2833> PMID: 20445542
14. Morrison I, Bjornsdotter M, Olausson H. Vicarious Responses to Social Touch in Posterior Insular Cortex Are Tuned to Pleasant Caressing Speeds. *J Neurosci.* 2011; 31: 9554–9562. <https://doi.org/10.1523/JNEUROSCI.0397-11.2011> PMID: 21715620
15. Essick GK, James A, McGlone FP. Psychophysical assessment of the affective components of non-painful touch. *Neuroreport.* 1999; 10: 2083–2087. <https://doi.org/10.1097/00001756-199907130-00017> PMID: 10424679
16. Löken LS, Wessberg J, Morrison I, McGlone F, Olausson H. Coding of pleasant touch by unmyelinated afferents in humans. *Nat Neurosci.* 2009; 12: 547–548. <https://doi.org/10.1038/nn.2312> PMID: 19363489
17. Lloyd DM, Gillis V, Lewis E, Farrell MJ, Morrison I. Pleasant touch moderates the subjective but not objective aspects of body perception. *Front Behav Neurosci.* 2013; 7: 207. <https://doi.org/10.3389/fnbeh.2013.00207> PMID: 24391563
18. Morrison I, Löken LS, Minde J, Wessberg J, Perini I, Nennesmo I, et al. Reduced C-afferent fibre density affects perceived pleasantness and empathy for touch. *Brain.* 2011; 134: 1116–1126. <https://doi.org/10.1093/brain/awr011> PMID: 21378097
19. Devine SL, Walker SC, Makdani A, Stockton ER, McFarquhar MJ, McGlone FP, et al. Childhood Adversity and Affective Touch Perception: A Comparison of United Kingdom Care Leavers and Non-care Leavers. *Front Psychol.* 2020; 11. <https://doi.org/10.3389/fpsyg.2020.557171> PMID: 33240148

20. Bales KL, Witczak LR, Simmons TC, Savidge LE, Rothwell ES, Rogers FD, et al. Social touch during development: Long-term effects on brain and behavior. *Neurosci Biobehav Rev.* 2018; 95: 202–219. <https://doi.org/10.1016/j.neubiorev.2018.09.019> PMID: 30278194
21. Walker SC, McGlone FP. The social brain: Neurobiological basis of affiliative behaviours and psychological well-being. *Neuropeptides.* 2013; 47. <https://doi.org/10.1016/j.npep.2013.10.008> PMID: 24210942
22. McGlone F, Wessberg J, Olausson H. Discriminative and Affective Touch: Sensing and Feeling. *Neuron.* 2014; 82: 737–755. <https://doi.org/10.1016/j.neuron.2014.05.001> PMID: 24853935
23. Jönsson EH, Kotilahti K, Heiskala J, Wasling HB, Olausson H, Croy I, et al. Affective and non-affective touch evoke differential brain responses in 2-month-old infants. *Neuroimage.* 2018; 169: 162–171. <https://doi.org/10.1016/j.neuroimage.2017.12.024> PMID: 29242105
24. Tuulari JJ, Scheinin NM, Lehtola S, Merisaari H, Saunavaara J, Parkkola R, et al. Neural correlates of gentle skin stroking in early infancy. *Dev Cogn Neurosci.* 2017 [cited 28 Nov 2018]. <https://doi.org/10.1016/j.dcn.2017.10.004> PMID: 29241822
25. Croy I, Luong A, Triscoli C, Hofmann E, Olausson H, Sailer U. Interpersonal stroking touch is targeted to C tactile afferent activation. *Behav Brain Res.* 2016; 297: 37–40. <https://doi.org/10.1016/j.bbr.2015.09.038> PMID: 26433145
26. Van Puyvelde M, Gorissen AS, Pattyn N, McGlone F. Does touch matter? The impact of stroking versus non-stroking maternal touch on cardio-respiratory processes in mothers and infants. *Physiol Behav.* 2019; 207: 55–63. <https://doi.org/10.1016/j.physbeh.2019.04.024> PMID: 31047950
27. Van Puyvelde M, Collette L, Gorissen AS, Pattyn N, McGlone F. Infants autonomic cardio-respiratory responses to nurturing stroking touch delivered by the mother or the father. *Front Physiol.* 2019; 10: 1117. <https://doi.org/10.3389/fphys.2019.01117> PMID: 31555148
28. Miguel HO, Gonçalves ÓF, Sampaio A. Behavioral response to tactile stimuli relates to brain response to affective touch in 12-month-old infants. *Dev Psychobiol.* 2020; 62: 107–115. <https://doi.org/10.1002/dev.21891> PMID: 31298419
29. Miguel HO, Gonçalves ÓF, Cruz S, Sampaio A. Infant brain response to affective and discriminative touch: A longitudinal study using fNIRS. *Soc Neurosci.* 2019; 14: 571–582. <https://doi.org/10.1080/17470919.2018.1536000> PMID: 30352004
30. Miguel HO, Lisboa IC, Gonçalves OF, Sampaio A. Brain mechanisms for processing discriminative and affective touch in 7-month-old infants. *Dev Cogn Neurosci.* 2019; 35: 20–27. <https://doi.org/10.1016/j.dcn.2017.10.008> PMID: 29108882
31. Pirazzoli L, Lloyd-Fox S, Braukmann R, Johnson MH, Gliga T. Hand or spoon? Exploring the neural basis of affective touch in 5-month-old infants. *Dev Cogn Neurosci.* 2019; 35: 28–35. <https://doi.org/10.1016/j.dcn.2018.06.002> PMID: 30120030
32. Fairhurst MT, Löken L, Grossmann T. Physiological and behavioral responses reveal 9-month-old infants' sensitivity to pleasant touch. *Psychol Sci.* 2014; 25: 1124–1131. <https://doi.org/10.1177/0956797614527114> PMID: 24681587
33. Croy I, Sehlstedt I, Wasling HB, Ackerley R, Olausson H. Gentle touch perception: From early childhood to adolescence. *Dev Cogn Neurosci.* 2019; 35: 81–86. <https://doi.org/10.1016/j.dcn.2017.07.009> PMID: 28927641
34. Ackerley R, Saar K, McGlone F, Backlund Wasling H. Quantifying the sensory and emotional perception of touch: differences between glabrous and hairy skin. *Front Behav Neurosci.* 2014; 8: 34. <https://doi.org/10.3389/fnbeh.2014.00034> PMID: 24574985
35. Essick GK, McGlone F, Dancer C, Fabricant D, Ragin Y, Phillips N, et al. Quantitative assessment of pleasant touch. *Neurosci Biobehav Rev.* 2010; 34: 192–203. <https://doi.org/10.1016/j.neubiorev.2009.02.003> PMID: 19896001
36. Kennedy WR, Wendelschafer-Crabb G, Polydefkis M, McArthur JC. Pathology and Quantitation of Cutaneous Innervation. *Peripher Neuropathy.* 2005; 1: 869–895. <https://doi.org/10.1016/B978-0-7216-9491-7.50037-5>
37. Liu Q, Vrontou S, Rice FL, Zylka MJ, Dong X, Anderson DJ. Molecular genetic visualization of a rare subset of unmyelinated sensory neurons that may detect gentle touch. *Nat Neurosci.* 2007; 10: 946–8. <https://doi.org/10.1038/nn1937> PMID: 17618277
38. Maruyama K, Shimoju R, Ohkubo M, Maruyama H, Kurosawa M. Tactile skin stimulation increases dopamine release in the nucleus accumbens in rats. *J Physiol Sci.* 2012; 62: 259–266. <https://doi.org/10.1007/s12576-012-0205-z> PMID: 22411566
39. Vrontou S, Wong AM, Rau KK, Koerber HR, Anderson DJ. Genetic identification of C fibres that detect massage-like stroking of hairy skin in vivo. *Nature.* 2013; 493: 669–73. <https://doi.org/10.1038/nature11810> PMID: 23364746

40. Pawling R, Trotter PD, McGlone FP, Walker SC. A positive touch: C-tactile afferent targeted skin stimulation carries an appetitive motivational value. *Biol Psychol*. 2017; 129. <https://doi.org/10.1016/j.biopsycho.2017.08.057> PMID: 28865933
41. Pawling R, Cannon PR, McGlone FP, Walker SC. C-tactile afferent stimulating touch carries a positive affective value. *PLoS One*. 2017; 12. <https://doi.org/10.1371/journal.pone.0173457> PMID: 28282451
42. Bourinet E, Martin M, Huzard D, Jeanneteau F, Mery P-F, François A. The impact of C-Tactile Low threshold mechanoreceptors on affective touch and social 1 interactions in mice. 2 3. *bioRxiv*. 2021; 2021.01.13.426492. <https://doi.org/10.1101/2021.01.13.426492>
43. Walker SC, Trotter PD, Woods A, McGlone F. Vicarious ratings of social touch reflect the anatomical distribution & velocity tuning of C-tactile afferents: A hedonic homunculus? *Behav Brain Res*. 2017; 320. <https://doi.org/10.1016/j.bbr.2016.11.046> PMID: 27915070
44. Löken LS, Evert M, Wessberg J. Pleasantness of touch in human glabrous and hairy skin: Order effects on affective ratings. *Brain Res*. 2011; 1417: 9–15. <https://doi.org/10.1016/j.brainres.2011.08.011> PMID: 21907328
45. Cascio CJ, Lorenzi J, Baranek GT. Self-reported Pleasantness Ratings and Examiner-Coded Defensiveness in Response to Touch in Children with ASD: Effects of Stimulus Material and Bodily Location. *J Autism Dev Disord*. 2016; 46: 1528–1537. <https://doi.org/10.1007/s10803-013-1961-1> PMID: 24091471
46. Decety J, Michalska KJ, Akitsuki Y. Who caused the pain? An fMRI investigation of empathy and intentionality in children. *Neuropsychologia*. 2008; 46: 2607–2614. <https://doi.org/10.1016/j.neuropsychologia.2008.05.026> PMID: 18573266
47. Suvilehto JT, Glerean E, Dunbar RIM, Hari R, Nummenmaa L. Correction for Suvilehto et al., Topography of social touching depends on emotional bonds between humans. *Proc Natl Acad Sci*. 2015; 112: E6718–E6718. <https://doi.org/10.1073/pnas.1521810112> PMID: 26598682
48. Heslin R, Nguyen TD, Nguyen ML. Meaning of touch: The case of touch from a stranger or same sex person. *J Nonverbal Behav*. 1983; 7: 147–157. <https://doi.org/10.1007/BF00986945>
49. Voos AC, Pelphrey KA, Kaiser MD. Autistic traits are associated with diminished neural response to affective touch. *Soc Cogn Affect Neurosci*. 2013; 8: 378–386. <https://doi.org/10.1093/scan/nss009> PMID: 22267520
50. Schaefer M, Heinze HJ, Rotte M. Embodied empathy for tactile events: Interindividual differences and vicarious somatosensory responses during touch observation. *Neuroimage*. 2012; 60: 952–957. <https://doi.org/10.1016/j.neuroimage.2012.01.112> PMID: 22306799
51. Schaefer M, Heinze H-J, Rotte M. Touch and personality: Extraversion predicts somatosensory brain response. *Neuroimage*. 2012; 62: 432–438. <https://doi.org/10.1016/j.neuroimage.2012.05.004> PMID: 22584236
52. Cascio CJ, Moore D, McGlone F. Social touch and human development. *Dev Cogn Neurosci*. 2019; 35: 5–11. <https://doi.org/10.1016/j.dcn.2018.04.009> PMID: 29731417
53. Kaiser MD, Yang DY-J, Voos AC, Bennett RH, Gordon I, Pretzsch C, et al. Brain Mechanisms for Processing Affective (and Nonaffective) Touch Are Atypical in Autism. *Cereb Cortex*. 2015; bhv125-. <https://doi.org/10.1093/cercor/bhv125> PMID: 26048952
54. Björnsdotter M, Löken L, Olausson H, Vallbo A, Wessberg J. Somatotopic organization of gentle touch processing in the posterior insular cortex. *J Neurosci*. 2009; 29: 9314–9320. <https://doi.org/10.1523/JNEUROSCI.0400-09.2009> PMID: 19625521
55. Brooks JCW, Zambreanu L, Godinez A., Craig A. D, Tracey I. Somatotopic organisation of the human insula to painful heat studied with high resolution functional imaging. *Neuroimage*. 2005; 27: 201–209. <https://doi.org/10.1016/j.neuroimage.2005.03.041> PMID: 15921935
56. Henderson LA., Rubin TK, Macefield VG. Within-limb somatotopic representation of acute muscle pain in the human contralateral dorsal posterior insula. *Hum Brain Mapp*. 2011; 32: 1592–1601. <https://doi.org/10.1002/hbm.21131> PMID: 20845392
57. Davidovic M, Jönsson EH, Olausson H, Björnsdotter M. Posterior superior temporal sulcus responses predict perceived pleasantness of skin stroking. *Front Hum Neurosci*. 2016; 10: 1–7.
58. Rolls ET. Sensory processing in the brain related to the control of food intake. *Proceedings of the Nutrition Society*. *Proc Nutr Soc*; 2007. pp. 96–112. <https://doi.org/10.1017/S0029665107005332> PMID: 17343776
59. Guest S, Grabenhorst F, Essick G, Chen Y, Young M, McGlone F, et al. Human cortical representation of oral temperature. *Physiol Behav*. 2007; 92: 975–984. <https://doi.org/10.1016/j.physbeh.2007.07.004> PMID: 17689575
60. Gazzola V, Spezio ML, Etzel J A., Castelli F, Adolphs R, Keysers C. Primary somatosensory cortex discriminates affective significance in social touch. *Proc Natl Acad Sci*. 2012; 109: E1657–E1666. <https://doi.org/10.1073/pnas.1113211109> PMID: 22665808