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High frequency heart rate variability is associated with sensitivity to affective touch

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ABSTRACT

C-tactile afferents (CTs) are a class of unmyelinated, mechanosensitive nerve fibre that respond optimally to skin temperature, slow moving touch typical of a caress. They are hypothesised to signal the rewarding value of affiliative tactile interactions. While CT firing frequency is positively correlated with subjective ratings of touch pleasantness, trait differences in sensitivity to the specific hedonic value of CT targeted touch have been reported.

Inter-individual differences in vagally mediated, high frequency heart rate variability (HF-HRV) have been linked to variation in visual social cognition. Thus, the aim of the present study was to examine the relationship between resting state HF-HRV and sensitivity to socially relevant CT targeted touch.

58 healthy participants first had a 5-minute electrocardiogram. They then rated the pleasantness of 5 randomly presented velocities of robotically delivered touch. Three velocities fell within (1, 3, 10 cm/s) and two outside (0.3, 30 cm/s) the CT optimal range. Each velocity was delivered twice.

On a group level, affective touch ratings were described by a negative quadratic function, with CT optimal velocities rated as more pleasant than slower and faster speeds. Simple regression analysis confirmed participants' HF-HRV was significantly predicted by the quadratic curve fit of their touch ratings, with higher HF-HRV associated with a better quadratic fit.

These findings indicate that, in line with previous observations that higher HF-HRV is associated with enhanced sensitivity to visual social cues, trait differences in autonomic control could account for previously reported individual differences in CT sensitivity.

1. Introduction

Positive social bonds promote resilience and enhance well-being, while social isolation and loneliness are significant risk factors for poor physical and mental health [1–4]. Altered social functioning, including changes in the perception of and sensitivity to social cues, is a hallmark of a range of mental health conditions [5]. While to date studies of social cognition have primarily focused on visual cues, particularly facial expressions, social interactions occur in a multisensory environment and vocal, olfactory, and tactile cues also contribute to social perception [6].

Touch is the first sense to develop and is fundamental to early infant-caregiver interactions [7,8]. Indeed, nurturing touch has been proposed to provide a sensory foundation on which social cognitive development is built [9–11]. Over the past decade, the role a specific subclass of

somatosensory afferent plays in the formation and maintenance of mammalian social bonds has received a great deal of attention [12]. C-tactile afferents (CTs) are unmyelinated, low threshold mechanosensitive nerves which respond optimally to a low force, low velocity (1–10 cm/s), skin temperature stimulus [13,14]. The observation that CT firing frequency correlates positively with subjective ratings of touch pleasantness led to the affective touch hypothesis that CTs signal the rewarding value of affiliative touch [15,16]. Indirect support for this hypothesis comes from observational studies which show that people spontaneously caress their loved ones using velocities that optimally activate CTs [17,18,21]. Furthermore, such CT targeted touch reduces autonomic arousal and buffers against the physiological and behavioural consequences of stress [19–22].

Psychophysical studies of affective touch demonstrate a negative quadratic relationship between touch velocity and perceived

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pleasantness across skin sites [23–25], with higher ratings given to CT optimal velocities between 1–10 cm/s than to slower or faster strokes. While this classic hedonic function is reliably observed on a group level, stable individual differences have also been reported [26–29], with some people showing a linear and others a random relationship between stroking velocity and perceived pleasantness. Such large inter-individual variation in hedonic functions is common across sensory systems and can reflect measurement error, as well as sensory and cognitive level factors including state and trait differences between participants [30, 31].

Changes in affective touch perception have been reported across a range of clinical populations including anorexia nervosa [32], autism [33], and depression [34], though other studies have found no clear relationship between individual differences in affective touch sensitivity and mental health diagnoses [17]. Interestingly, self-reported previous and current experiences of social touch appear to be reliably associated with psychophysical measures of affective touch perception [29,34,35]. Indeed, further evidence a person's social history shapes their psychophysical ratings of affective touch comes from studies reporting both insecure attachment and childhood adversity are associated with blunted ratings of CT optimal touch [36,37]. Taken together this literature indicates that cognitive factors account in part for individual differences in CT sensitivity, however their specific nature remains unknown.

Heart rate variability (HRV), that is beat-to-beat changes in heart rate, is an indirect, well-validated index of vagal modulation [38]. Higher levels of resting HRV, reflecting higher parasympathetic nervous system activity, are associated with better emotional and behavioural regulation and enhanced health and well-being [39,40]. Clinically, low levels of vagally mediated HRV (vmHRV) have been associated with a range of mental health conditions, including depression [39,41]. Socially, while secure attachment has been linked to higher efficiency in vmHRV and cognitive abilities [42], childhood trauma and attachment insecurity have been reported to predict reduced vmHRV [43]. Indeed, there is evidence people with higher levels of resting state vmHRV are more successful at forming and maintaining social relationships [44,45], while chronic loneliness predicts lower vmHRV [46].

Several influential bio-behavioural models posit that the autonomic nervous system (ANS) functions to support mammalian social engagement [47,48]. For example, the neurovisceral integration model [49] posits that vmHRV is an index of the engagement of prefrontal brain networks during emotional and cognitive processing. Accordingly, enhanced ability of people with higher resting vmHRV to form and maintain social relationships is proposed to reflect adaptive perceptual and attentional responses to social cues [50,51]. A variety of experimental studies also provide support for the relationship between measures of vmHRV and facial emotion recognition based on performance of the widely used, Reading the Mind in the Eyes task [52]. Specifically, it appears to be greater sensitivity to positive rather than negative emotional cues in other's faces which underpins this association [53], supporting the notion people higher in vmHRV display higher levels of approach motivation. In addition to making judgements about higher order mental states, people make rapid attributions about signals of safety and threat from faces [54] and in a recent study higher levels of resting vmHRV were associated with more positive ratings of the trustworthiness of stranger's faces [55].

It has been proposed that affective touch, as with faces, can act as social signal of safety and proximity [56]. Given studies to date indicate social and cognitive factors account for some inter-individual differences in hedonic ratings of CT targeted affective touch, the aim of the present study was to determine whether autonomic nervous system function, as indexed by resting state vmHRV, also predicts affective sensitivity to CT targeted touch.

2. Methods

2.1. Participants

Participants were 64 students recruited through email advertising from Liverpool John Moores University (LJMU). Participants all provided written informed consent before completing the study and received a £10 shopping voucher as compensation for their time. The study received ethical clearance from LJMU Research Ethics committee (15/NSP/004).

Participants were excluded from participation if they had an allergy to sticking plasters, a heart condition, or were currently taking cardiac, antipsychotic, antihypertensive or antidepressant medication.

Of the original sample, six participants were lost, two due to failure of either the touch robot or participant PC, two due to failure to follow instructions, one due to excessive noise in their ECG and one due to missing questionnaire data. The final sample therefore consisted of 58 participants of whom 38 were female and 20 male. The mean age of the sample was 22.3 years (SD = 3.7 years).

2.2. Measures

2.2.1. Heart rate variability

A three lead ECG was used to record heart rate during a 5 minute baseline period. Disposable electrodes were placed just below the participant's left and right clavicle and above their left hip. Data were digitised using an AD Instruments PowerLab recording from an AD Instruments BioAmp. The ECG trace was sampled at 2000 Hz and offline bandpass filtered between 5 Hz and 30 Hz before being exported as a tab delimited text file. Vagal tone can be estimated using HRV measured in the time domain using calculations such as the root mean square of successive beat-to-beat intervals (IBIs) or by extracting the high-frequency component of the power spectrum once a series of IBIs has been transformed into the frequency domain [57]. HF-HRV is one valid operationalisation of vmHRV [58] that has been used in previous relevant studies [53,59]. Kubios (version 2.2, Kubios Oy, Kuopio, Finland) was used to extract values for the percentage of the heart rate variability power spectrum represented by the high-frequency bandwidth of 0.15–0.40 Hz (HF-HRV).

2.2.2. Touch stimuli

To remove confounding social factors and to precisely control the velocity, pressure and onset of the touch stimuli, a specially designed robot, or 'Rotary Tactile Stimulator' (RTS – Dancer Design) was used. The RTS uses online speed and force feedback to deliver precise velocities and pressures of touch, administered with an 'arm' ending in a soft brush tip (Boots No.7). The RTS was pre-programmed to deliver touch stimuli at velocity 0.3, 1, 3, 10 and 30 cm/second, with constant pressure of 0.3 N. Each 'stroke' from the RTS covered an aperture of approximately 8.1 cm, with the five velocities of touch taking approximately 27, 8.1, 2.7, 0.8 and 0.3 seconds respectively to cover the aperture. The velocities and pressure were chosen to include what microneurography-based research indicates to be the optimal quality of touch to activate CT's, velocities of between 1 and 10 cm/second [13, 14], as well as control velocities outside of this range. In the current experiment the RTS delivered touch stimuli to the volar surface of the forearm, an area of hairy skin innervated by CTs [14]. The onset of each stimulus was controlled by the computer on which the participants completed their ratings of touch pleasantness. This machine sent a transistor-transistor logic (TTL) trigger down a parallel port cable to activate the RTS each time a touch stimulus was to be delivered.

2.2.3. Touch ratings

Touch rating scales were presented using EPrime (Psychology Software Tools, Sharpsburg, PA, USA). The scale consisted of an unbroken horizontal line anchored with the values -10 and +10 at the left and

right ends respectively, and with the words ‘unpleasant’ and ‘pleasant’ in the same respective locations. The numerical anchors were provided as an additional aid to participants when deciding how pleasant they found each touch stimulus, but the scale recorded the participant’s click in an analogue manner with possible scores ranging from 0 at the unpleasant extreme and 99 at the pleasant extreme, in increments of one.

2.2.4. International physical activity questionnaire (IPAQ)

[60]: All participants completed an adapted paper version of the IPAQ which assessed their levels of regular physical activity over the last three months. The questions in the IPAQ focused on regularity and duration per week of vigorous and medium intensity exercise, walking and sitting. Following the protocol described by [61] participant’s responses were translated into MET-minutes per week. Here each type of activity is weighted by its energy requirements, (MET = multiples of the resting metabolic rate). A MET-minute is computed by multiplying the MET score by the minutes performed.

2.3. Procedure

Upon entering the laboratory participants were briefed about the upcoming tasks. Participants completed the IPAQ and were then fitted with ECG electrodes. They sat in a comfortable reclining chair with a computer screen suspended in front of them. They were given a lap tray on which a keyboard and mouse were placed. Next baseline ECG was recorded while the participant relaxed and watched a five-minute clip from a nature documentary featuring coral reefs and fish, with an audio commentary (i.e. “vanilla baseline” [62]). After the baseline recording the experimenter placed the participant’s left arm on a vac-cushion arm rest so that the arm was comfortably outstretched horizontally, with the palm turned upwards so that the inner surface of the forearm could be stimulated by the RTS. The air was removed from the vac-cushion to fix the participant’s arm in place, before the RTS probe (brush) was lowered into place and calibrated.

After the RTS had been calibrated, the participants were familiarised with the rating scale used to record perceptions of touch pleasantness. The Touch Task consisted of 10 stimulations, with each of the 5 velocities repeated twice. The presentation order of the touch stimuli was quasi-randomised so that it consisted of two blocks of five stimulations, with each block containing all five velocities in a random order. Each trial began with a 2000 ms fixation cross presented centrally on the computer screen in front of the participant. The participants were instructed to look at the cross when it appeared and to remain looking at the screen and not the RTS during stimulation. The fixation cross was followed by the onset of the touch stimulus, immediately after which the rating scale was presented on screen. After the participant had responded, by using the mouse to click on the appropriate location on the rating scale, the screen changed to a ‘please relax’ message, which lasted for 28,000 ms, minus the participant’s response time to the scale. This meant that in combination with the fixation period, each touch stimulus was separated from the previous stimulus by an ISI of 30 seconds.

After completing the Touch Task, the ECG electrodes were removed, and the participant moved to a second PC where they completed a short series of cognitive tasks (data not reported here). Upon completion of this last section of the study the participant was debriefed and provided with their compensatory payment.

2.4. Data processing and analysis

2.4.1. Touch rating response analysis

Ratings of the five velocities of touch were expected to reflect the negative quadratic shape described in the introduction, with higher ratings given to CT optimal stimuli (1, 3 and 10 cm/second) than non-CT-optimal stimuli (0.3 and 30 cm/second). To test for the presence of this pattern of ratings, mean ratings for each velocity were calculated at the participant level by averaging across their two ratings of each

stimulus. These ratings were entered into a repeated measures ANOVA (anova_test, rstatix package, r 4.2.3) with the within participants variable of Velocity (0.3, 1, 3, 10, 30) and the dependent variable of mean rating. Greenhouse-Geisser correction was used to account for violations of sphericity. Post-hoc Bonferroni corrected *t*-tests were used to perform pairwise comparisons of the different touch velocities (pairwise_t_test, rstatix package, r 4.2.3). Before this analysis was conducted, data from three participants who were identified as outliers in the main analysis (as described below) were removed.

2.4.2. Relationship between heart rate variability and CT touch sensitivity

To examine the relationship between HF-HRV levels and sensitivity to CT touch, HF-HRV was regressed against coefficients representing the fit of each participants’ touch ratings to the linear and quadratic terms of a regression model. It was expected that HF-HRV levels would be positively related to the strength of the quadratic fit, but not the linear fit.

The first stage in the analysis involved the extraction of outliers from the HF-HRV scores, which lead to the removal of two participants whose scores were lower than the first quartile or higher than the third quartile by 1.5 times the inter-quartile range. Next the influence of three non-psychological factors that might affect HF-HRV [63] – the participant’s age, sex and exercise levels in MET-minutes per week – were controlled for. To achieve this, HF-HRV scores for the remaining 56 participants were entered as the output variable into a multiple regression (lm, r 4.2.3) with age, a dummy coded sex variable, and MET-minutes as predictors. Standardised residuals from this model were saved (HF-HRV_{std}), as per Quintana et al [59].

Following a similar approach to that used in Ali et al. [35] beta-coefficients for the fit of each participants’ touch ratings to a linear and quadratic term were generated in R. An outlier analysis of the quadratic and linear coefficients lead to the removal of one further participant because their quadratic score was lower than the first quartile by more than 1.5 times the interquartile range. The remaining 55 participants’ data were entered into a hierarchical regression where the first model tested whether Quadratic Fit predicted HF-HRV_{std}, and the second model tested whether Quadratic Fit + Linear Fit predicted HF-HRV_{std}.

3. Results

Descriptive statistics are presented in Table 1 and Pearson’s correlations between variables are presented in Table 2.

The analysis of the touch ratings across all participants revealed the expected main effect of Velocity, $F(2.62, 141.52) = 14.3, p < .001, \eta^2 = 0.21$, reflecting the negative quadratic pattern shown in Fig. 1. Post-hoc comparisons showed that touch at all CT-optimal velocities was rated as more pleasant than non-CT optimal touch (corrected *ps* < 0.005), except for the comparison of 1 cm/second and 30 cm/second (*p* = .19). All CT optimal velocities were rated as similarly pleasant, as were non-CT optimal velocities. As such, the robotically delivered touch stimuli resulted in the expected pattern of ratings, reflecting the higher hedonic quality of CT optimal touch.

We next explored whether individual differences in sensitivity to the hedonic quality of CT touch (quadratic fit of touch ratings) might be related to levels of vagal modulation (HF-HRV). Quadratic Fit was a significant predictor of HF-HRV, $F(1,53) = 4.8, p = .034$, accounting for

Table 1
Descriptive statistics.

Variable	Mean	SD
Age (years)	22.11	3.50
MET Mins	5462.85	3605.69
HF-HRV	30.47	17.04
HF-HRV _{std}	-0.0085	1.0070

Table 2
Correlations between variables.

	Age	Sex	MET Mins	Quad Fit	Lin Fit	HF-HRV
Sex	-0.10					
MET Mins	-0.27*	.0011				
Quad Fit	.085	-0.073	.26			
Lin Fit	-0.024	-0.19	-0.12	.22		
HF-HRV	-0.11	-0.14	.027	.29*	.038	

* $p < .05$ ** $p < .001$

8.2% of the variance (adjusted $R^2 = 0.07$), $\beta = 0.069$, $\beta \text{ SE} = 0.031$, $p = .034$. Analysis of variance revealed that a second model including both Quadratic Fit and Linear Fit as predictors of HF-HRV did not provide significantly improved predictive power ($p = .85$). In this second model, which accounted for 8.3% of the variance (adjusted $R^2 = 0.05$), Quadratic Fit remained a significant predictor of HF-HRV, $\beta = 0.070$, $\beta \text{ SE} = 0.033$, $p = .036$, but Linear Fit was not in its own right predictive of HF-HRV, $\beta = 0.0034$, $\beta \text{ SE} = 0.018$, $p = .85$.

This analysis was repeated using the scores for HF-HRV_{std}. Again, a model using just the Quadratic Fit scores to predict HF-HRV_{std} was significant, $F(1,53) = 4.4$, $p = .040$, accounting for 7.7% of the variance (adjusted $R^2 = 0.06$), $\beta = 0.004$, $\beta \text{ SE} = 0.001$, $p = .040$, and a model using both the Quadratic Fit and Linear Fit scores which accounted for 8.3% of the variance (adjusted $R^2 = 0.05$), did not significantly improve predictive power ($p = .67$). In this second model, Quadratic Fit remained a significant predictor of HF-HRV_{std}, $\beta = 0.004$, $\beta \text{ SE} = 0.0019$, $p = .038$, but Linear Fit was not in its own right predictive of HF-HRV_{std}, $\beta = 0.00046$, $\beta \text{ SE} = 0.0011$, $p = .67$. The relationship between HF-HRV_{std} and Quadratic Fit scores can be seen in Fig. 2. The results support the notion that higher levels of vagal modulation, as indexed by HF-HRV, are associated with greater sensitivity to the hedonic quality of CT touch.

4. Discussion

In this study, we investigated whether inter-individual differences in sensitivity to the specific hedonic value of CT optimal touch are

positively associated with individual variation on HF-HRV. Consistent with previous studies, when averaged across the whole sample, we saw the standard negative quadratic relationship between touch velocity and perceived pleasantness, with CT optimal touch rated as more pleasant than faster or slower strokes. We also found that the degree to which a participant's ratings of the different touch velocities fitted a negative quadratic curve positively predicted resting state HF-HRV, indicating increased affective-tactile discrimination with increasing autonomic nervous system regulation.

Several previous studies have reported stable individual differences in sensitivity to CT touch [26,28,64], however mechanistic explanations for this variation are currently lacking. The present findings indicate that variation in vmHRV can account for some of the individual differences seen. The rationale for the present study was grounded in the affective touch hypothesis of CT function which posits CTs signal the rewarding value of affiliative tactile interactions and thus, through early nurturing experiences, support the formation and maintenance of mammalian social bonds [15,16]. There is indirect support for this hypothesis in that CT optimal velocities of touch are ecologically relevant, reduce physiological arousal and hedonic ratings are grounded in developmental experiences of CT input [17,18,21,65,66]. Higher vmHRV is associated with greater sensitivity to visual social cues, particularly positive ones and is proposed to result in greater approach motivation, perhaps explaining the apparently enhanced ability of those with high vmHRV to form and maintain social relationships [44,52,55]. The present findings suggest that sensitivity to the hedonic value of socially relevant touch is also enhanced in people with higher levels of resting vmHRV. However, future studies are required which replicate and extend the present one to determine whether, consistent with our proposal, vmHRV predicts sensitivity to both CT targeted touch and facial cues in the same study. Furthermore, social interactions depend on interpreting the emotional states of others and this capacity is in part dependent on a person's ability to interpret their own emotional state, termed alexithymia [67]. It has previously been found that individuals with high HF-HRV show less alexithymia than individuals with low HF-HRV [50]. Thus, it could be that levels of alexithymia mediate the relationship between HF-HRV, and both facial emotion recognition and

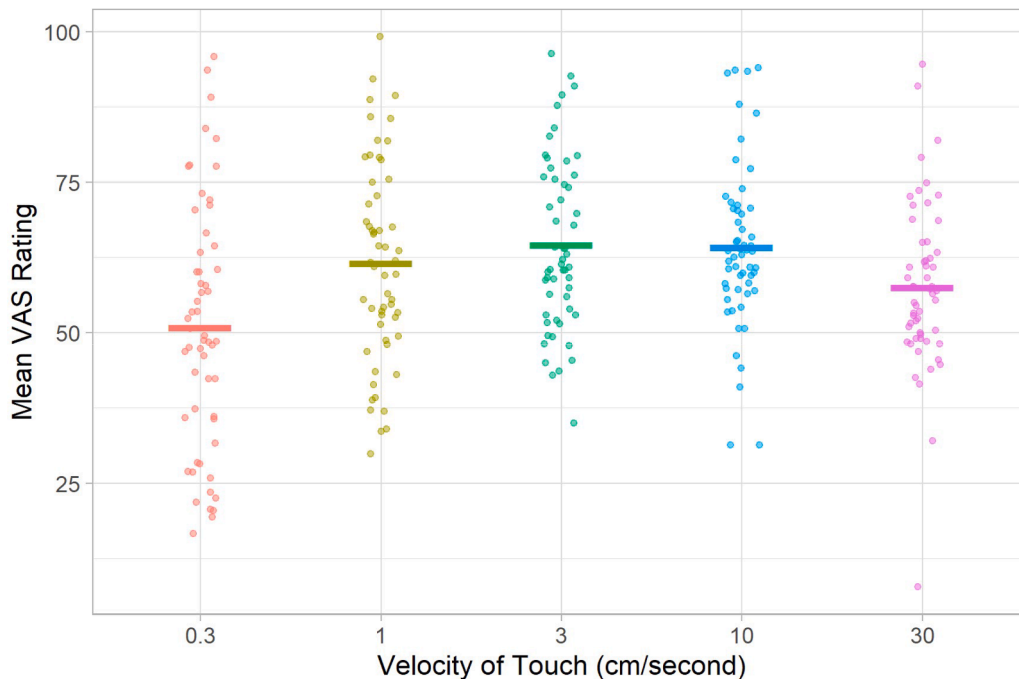


Fig. 1. Mean ratings of pleasantness on a 100-point VAS scale (where 0 = unpleasant and 99 = pleasant), in response to each of the five velocities of touch. Dots represent the mean rating for individual participants (averaged over two ratings of each velocity). Horizontal bars represent the sample mean for each velocity.

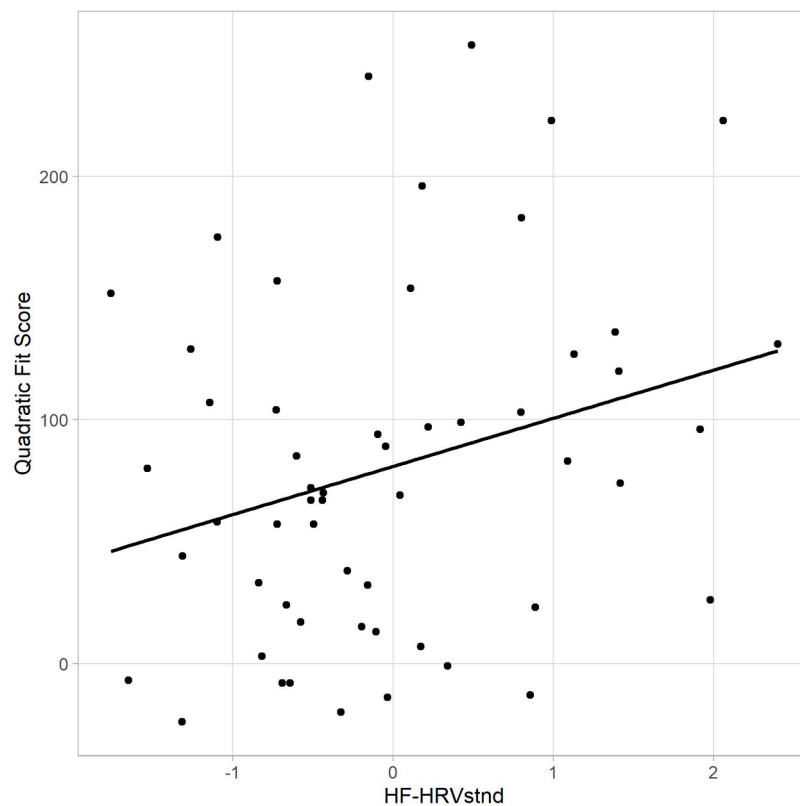


Fig. 2. Relationship between HF-HRV_{std} and Quadratic Fit Score. HF-HRV_{std} is the percentage HF-HRV adjusted for covariation with age, sex and exercise levels. Quadratic Fit Score is the beta- coefficient representing the extent to which the participant's ratings of touch could be predicted by the expected negative quadratic distribution.

CT sensitivity.

It is noteworthy that in psychophysical studies of affective touch, including the present one, ratings are made in a highly controlled experimental setting, stripped of the typical context in which social tactile interactions occur. Several studies have provided evidence a person's social world, past and present, shapes these ratings. For example, greater sensitivity to CT over non-CT optimal touch is seen in people who report more positive attitudes towards and greater experience of social touch [35,34], while insecure attachment and adverse childhood experiences are associated with both blunted ratings of CT optimal touch [36,37] and low levels of resting vmHRV [43]. Thus, while the utility of psychophysical ratings to specifically probe CT function, given the concomitant input from A β afferents, has been questioned [68], taken together these findings support the hypothesis judgements are in part shaped by affective evaluations of the sensory signal, grounded in past social experience.

While the effect size in the present study is small, with HF-HRV explaining just 8.2% of the variance in CT sensitivity, it is consistent with the extant literature reporting positive associations between vmHRV and social cognition. For example, a similarly designed study reported that HF-HRV accounted for 8.4% of variance in performance of the Reading the Mind in the Eyes task [59]. While controlling for exercise frequency, age and sex had no impact on our study findings, several other factors that could affect vmHRV, including medication, recent caffeine and food intake, as well as drug and alcohol use were not accounted for [52]. Furthermore, inferences around causality cannot be drawn from correlational studies such as this. A further limitation of the present study is the fact our sample were all healthy young adults; thus, it remains to be determined whether the study findings generalise to older adults or clinical populations.

As previous studies have reported affective touch perception is atypical in anorexia [32], autism [33] and depression [34], and atypical

vmHRV has been reported in all three conditions [39,41,69,70], future between group studies should determine whether differences in HRV can account for any part of these findings. Also, while the present study considered the relationship between tonic levels of vmHRV and CT touch sensitivity, future experimental studies should investigate whether phasic changes in vmHRV heighten sensitivity to CT optimal over non-CT optimal touch. Additionally, it is noteworthy that CT optimal touch increases phasic vmHRV [20] and enhances ratings of approachability of previously neutral faces it is paired with [71]. Thus, it would be of interest to determine whether the mechanism by which affective touch modulates processing of subtle social cues, like facial trustworthiness, is mediated by touch induced changes in vmHRV.

In summary, this study provides evidence that autonomic nervous system function can explain some of the reported variation in sensitivity to CT targeted affective touch, a sensory input hypothesised to have a social developmental function. This relationship was observed even after controlling for a variety of variables that are known to influence vmHRV. As reduced vmHRV and blunted sensitivity to CT targeted touch has been reported in several clinical conditions, the results provide a trans-diagnostic mechanistic target for future investigation.

CRedit authorship contribution statement

Ralph Pawling: Writing – review & editing, Visualization, Methodology, Formal analysis. **Francis. McGlone:** Writing – review & editing, Funding acquisition, Conceptualization. **Susannah C. Walker:** Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

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References

- [1] J. Holt-Lunstad, Why social relationships are important for physical health: a systems approach to understanding and modifying risk and protection, *Annu. Rev. Psychol.* 69 (1) (2018) 437–458, <https://doi.org/10.1146/annurev-psych-122216-011902>.
- [2] N. Leigh-Hunt, D. Bagguley, K. Bash, V. Turner, S. Turnbull, N. Valtorta, W. Caan, An overview of systematic reviews on the public health consequences of social isolation and loneliness, *Publ. Health* 152 (2017) 157–171, <https://doi.org/10.1016/j.puhe.2017.07.035>.
- [3] M. Ungar, L. Theron, Resilience and mental health: how multisystemic processes contribute to positive outcomes, *Lancet Psych* 7 (5) (2020) 441–448, [https://doi.org/10.1016/S2215-0366\(19\)30434-1](https://doi.org/10.1016/S2215-0366(19)30434-1).
- [4] X. Zhang, S. Dong, The relationships between social support and loneliness: a meta-analysis and review, *Acta Psychol.* (Amst) 227 (2022) 103616, <https://doi.org/10.1016/j.actpsy.2022.103616>.
- [5] H. Santamaría-García, S. Baez, C. Gómez, O. Rodríguez-Villagra, D. Huepe, M. Portela, P. Reyes, J. Klahr, D. Matallana, A. Ibanez, The role of social cognition skills and social determinants of health in predicting symptoms of mental illness, *Transl. Psych* 10 (1) (2020) 165, <https://doi.org/10.1038/s41398-020-0852-4>.
- [6] M.M. Rogers-Carter, J.P. Christianson, An insular view of the social decision-making network, *Neurosci. Biobehav. Rev* 103 (2019) 119–132, <https://doi.org/10.1016/j.neubiorev.2019.06.005>.
- [7] I. Croy, M.T. Fairhurst, F. McGlone, The role of C-tactile nerve fibers in human social development, *Curr. Opin. Behav. Sci* 43 (2022) 20–26, <https://doi.org/10.1016/j.cobeha.2021.06.010>.
- [8] A. Fotopoulou, M. von Mohr, C. Krahé, Affective regulation through touch: homeostatic and allostatic mechanisms, *Curr. Opin. Behav. Sci* 43 (2022) 80–87, <https://doi.org/10.1016/j.cobeha.2021.08.008>.
- [9] K.L. Bales, L.R. Witzak, T.C. Simmons, L.E. Savidge, E.S. Rothwell, F.D. Rogers, R. A. Manning, M.J. Heise, M. Englund, R. Arias del Razo, Social touch during development: long-term effects on brain and behavior, *Neurosci. Biobehav. Rev* 95 (2018) 202–219, <https://doi.org/10.1016/j.neubiorev.2018.09.019>.
- [10] C. Cascio, D. Moore, F. McGlone, Social touch and human development, *Dev. Cogn. Neurosci* 35 (2019) 5–11, <https://doi.org/10.1016/j.dcn.2018.04.009>.
- [11] S.C. Walker, F. McGlone, The social brain: Neurobiological basis of affiliative behaviours and psychological well-being, *Neuropeptides* 47 (6) (2013), <https://doi.org/10.1016/j.npep.2013.10.008>.
- [12] A. Schirmer, F. McGlone, Editorial overview: affective touch: neurobiology and function, *Curr. Opin. Behav. Sci* 45 (2022) 101129, <https://doi.org/10.1016/j.cobeha.2022.101129>.
- [13] R. Ackerley, H. Backlund Wasling, J. Liljenkrantz, H. Olausson, R.D. Johnson, J. Wessberg, Human C-tactile afferents are tuned to the temperature of a skin-stroking caress, *J. Neurosci* 34 (8) (2014) 2879–2883, <https://doi.org/10.1523/JNEUROSCI.2847-13.2014>.
- [14] L.S. Löken, J. Wessberg, I. Morrison, F. McGlone, H. Olausson, Coding of pleasant touch by unmyelinated afferents in humans, *Nat. Neurosci* 12 (5) (2009) 547–548, <https://doi.org/10.1038/nn.2312>.
- [15] I. Morrison, L.S. Löken, H. Olausson, The skin as a social organ, *Exp. Brain Res* 204 (3) (2010) 305–314, <https://doi.org/10.1007/s00221-009-2007-y>.
- [16] H. Olausson, J. Wessberg, I. Morrison, F. McGlone, Å. Vallbo, The neurophysiology of unmyelinated tactile afferents, *Neurosci. Biobehav. Rev* 34 (2) (2010) 185–191, <https://doi.org/10.1016/j.neubiorev.2008.09.011>.
- [17] I. Croy, H. Geide, M. Paulus, K. Weidner, H. Olausson, Affective touch awareness in mental health and disease relates to autistic traits – an explorative neurophysiological investigation, *Psych. Res* 245 (2016) 491–496, <https://doi.org/10.1016/j.psychres.2016.09.011>.
- [18] M. Van Puyvelde, L. Collette, A.S. Gorissen, N. Pattyn, F. McGlone, Infants autonomic cardio-respiratory responses to nurturing stroking touch delivered by the mother or the father, *Front. Physiol* 10 (2019) 1117, <https://doi.org/10.3389/fphys.2019.01117>.
- [19] T. Kidd, S.L. Devine, S.C. Walker, Affective touch and regulation of stress responses, *Health Psychol. Rev* 17 (1) (2023) 60–77, <https://doi.org/10.1080/17437199.2022.2143854>.
- [20] C. Triscoli, I. Croy, S. Steudte-Schmiedgen, H. Olausson, U. Sailer, Heart rate variability is enhanced by long-lasting pleasant touch at CT-optimized velocity, *Biol. Psychol.* (2017), <https://doi.org/10.1016/j.biopsycho.2017.07.007>.
- [21] M. Van Puyvelde, A.S. Gorissen, N. Pattyn, F. McGlone, Does matter? The impact of stroking versus non-stroking maternal touch on cardio-respiratory processes in mothers and infants, *Physiol. Behav* 207 (2019) 55–63, <https://doi.org/10.1016/j.physbeh.2019.04.024>.
- [22] S.C. Walker, A. Cavieles, V. Peñaloza-Sancho, W. El-Deredey, F. McGlone, A. Dagnino-Subiabre, C-low threshold mechanoafferent targeted dynamic touch modulates stress resilience in rats exposed to chronic mild stress, *Europ. J. Neurosci* (2020) 1–14, <https://doi.org/10.1111/ejn.14951>.
- [23] R. Ackerley, I. Carlsson, H. Wester, H. Olausson, H. Backlund Wasling, Touch perceptions across skin sites: differences between sensitivity, direction discrimination and pleasantness, *Front. Behav. Neurosci* 8 (2014) 54, <https://doi.org/10.3389/fnbeh.2014.00054>.
- [24] G. Essick, A. James, F. McGlone, Psychophysical assessment of the affective components of non-painful touch, *Neuroreport* 10 (10) (1999) 2083–2087, <https://doi.org/10.1097/00001756-199907130-00017>.
- [25] G. Essick, F. McGlone, C. Dancer, D. Fabricant, Y. Ragin, N. Phillips, T. Jones, S. Guest, Quantitative assessment of pleasant touch, *Neurosci. Biobehav. Rev* 34 (2) (2010) 192–203, <https://doi.org/10.1016/j.neubiorev.2009.02.003>.
- [26] I. Croy, A. Bierling, U. Sailer, R. Ackerley, Individual variability of pleasantness ratings to stroking touch over different velocities, *Neuroscience* 464 (2021) 33–43, <https://doi.org/10.1016/j.neuroscience.2020.03.030>.
- [27] I. Croy, A. Luong, C. Triscoli, E. Hofmann, H. Olausson, U. Sailer, Interpersonal stroking touch is targeted to C tactile afferent activation, *Behav. Brain Res* 297 (2016) 37–40, <https://doi.org/10.1016/j.bbr.2015.09.038>.
- [28] L. Crucianelli, M. Chancel, H.H. Ehrsson, Modeling affective touch pleasantness across skin types at the individual level reveals a reliable and stable basic function, *J. Neurophysiol* 128 (6) (2022) 1435–1452, <https://doi.org/10.1152/jn.00179.2022>.
- [29] U. Sailer, R. Ackerley, Exposure shapes the perception of a ff ective touch, *Develop. Cogn. Neurosci* 35 (xxxx) (2017) 109–114.
- [30] J. Lim, Hedonic scaling: a review of methods and theory, *Food Qual. Prefer* 22 (8) (2011) 733–747, <https://doi.org/10.1016/j.foodqual.2011.05.008>.
- [31] H.R. Moskowitz, Sensory intensity versus hedonic functions: classical psychophysical approaches, *J. Food Qual* 5 (2) (1982) 109–137, <https://doi.org/10.1111/j.1745-4557.1982.tb00738.x>.
- [32] L. Crucianelli, V. Cardì, J. Treasure, P.M. Jenkinson, A. Fotopoulou, The perception of affective touch in anorexia nervosa, *Psych. Res* 239 (2016) 72–78, <https://doi.org/10.1016/j.psychres.2016.01.078>.
- [33] M.D. Kaiser, D.Y.J. Yang, A.C. Voos, R.H. Bennett, I. Gordon, C. Pretzsch, D. Beam, C. Keifer, J. Eilbott, F. McGlone, K.A. Pelphey, Brain mechanisms for processing affective (and nonaffective) touch are atypical in Autism, *Cerebral. Cortex* 26 (6) (2016) 2705–2714, <https://doi.org/10.1093/cercor/bhv125>.
- [34] V.C. Tinker, P.D. Trotter, C. Krahé, Depression severity is associated with reduced pleasantness of observed social touch and fewer current intimate touch experiences, *PLoS One* 18 (8) (2023) e0289226, <https://doi.org/10.1371/journal.pone.0289226>.
- [35] S.H. Ali, A.D. Makdani, M.I. Cordero, A.E. Paltoglou, A.G. Marshall, M. J. McFarquhar, F. McGlone, S.C. Walker, P.D. Trotter, Hold me or stroke me? Individual differences in static and dynamic affective touch, *PLoS One* 18 (5 May) (2023) 1–25, <https://doi.org/10.1371/journal.pone.0281253>.
- [36] S.L. Devine, S.C. Walker, A. Makdani, E.R. Stockton, M.J. McFarquhar, F. McGlone, P.D. Trotter, 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>.
- [37] C. Krahé, M. von Mohr, A. Gentsch, L. Guy, C. Vari, T. Nolte, A. Fotopoulou, Sensitivity to CT-optimal, affective touch depends on adult attachment style, *Sci Rep* 8 (1) (2018) 1–10, <https://doi.org/10.1038/s41598-018-32865-6>.
- [38] M. Pagani, F. Lombardi, R. Guzzetti, O. Rimoldi, R. Furlan, P. Pizzinelli, G. Sandrone, G. Malfatto, S. Dell’Orto, E. Piccaluga, Power spectral analysis of heart rate and arterial pressure variabilities as a marker of sympatho-vagal interaction in man and conscious dog, *Circ. Res* 59 (2) (1986) 178–193, <https://doi.org/10.1161/01.RES.59.2.178>.
- [39] T.P. Beauchaine, J.F. Thayer, Heart rate variability as a transdiagnostic biomarker of psychopathology, *Int. J. Psychophysiol* 98 (2) (2015) 338–350, <https://doi.org/10.1016/j.ijpsycho.2015.08.004>.
- [40] M.N. Jarczok, K. Weimer, C. Braun, D.P. Williams, J.F. Thayer, H.O. Gündel, E. M. Balint, Heart rate variability in the prediction of mortality: A systematic review and meta-analysis of healthy and patient populations, *Neurosci. Biobehav. Rev* 143 (2022) 104907, <https://doi.org/10.1016/j.neubiorev.2022.104907>.
- [41] M. Kidwell, B.A. Ellenbroek, Heart and soul: heart rate variability and major depression, *Behav. Pharmacol* 29 (2 and 3) (2018) 152–164, <https://doi.org/10.1097/FBP.0000000000000387>.
- [42] F. Ghafarimoghadam, F. Dehghani-Arani, Measurement of heart rate variability and cognitive abilities based on attachment styles in children with chronic medical conditions, *Sci. Rep* 9 (1) (2019) 5254, <https://doi.org/10.1038/s41598-019-41812-y>.
- [43] S.N. Back, M. Schmitz, J. Koenig, M. Zettl, N. Kleindienst, S.C. Herpertz, K. Bertsch, Reduced vagal activity in borderline personality disorder is unaffected by intranasal oxytocin administration, but predicted by the interaction between childhood trauma and attachment insecurity, *J. Neural Transm* 129 (4) (2022) 409–419, <https://doi.org/10.1007/s00702-022-02482-9>.
- [44] B.E. Kok, B.L. Fredrickson, Upward spirals of the heart: Autonomic flexibility, as indexed by vagal tone, reciprocally and prospectively predicts positive emotions and social connectedness, *Biol. Psychol* 85 (3) (2010) 432–436, <https://doi.org/10.1016/j.biopsycho.2010.09.005>.
- [45] S. Shahrestani, E.M. Stewart, D.S. Quintana, I.B. Hickie, A.J. Guastella, Heart rate variability during adolescent and adult social interactions: a meta-analysis, *Biol. Psychol* 105 (2015) 43–50, <https://doi.org/10.1016/j.biopsycho.2014.12.012>.
- [46] C.M. Roddick, F.S. Chen, Effects of chronic and state loneliness on heart rate variability in women, *Annals Behav. Med* 55 (5) (2021) 460–475, <https://doi.org/10.1093/abm/kaaa065>.
- [47] S.W. Porges, R.D. Lane, The polyvagal perspective, *Biol. Psychol.* 74 (2) (2007) 116–143.
- [48] J.F. Thayer, R.D. Lane, A model of neurovisceral integration in emotion regulation and dysregulation, *J. Affect. Disord.* 61 (3) (2000) 201–216.
- [49] J.F. Thayer, A.L. Hansen, E. Saus-Rose, B.H. Johnsen, Heart rate variability, prefrontal neural function, and cognitive performance: the neurovisceral

- integration perspective on self-regulation, adaptation, and health, *Annals Behav. Med* (2009), <https://doi.org/10.1007/s12160-009-9101-z>.
- [50] A. Lischke, R. Pahnke, A. Mau-Moeller, M. Behrens, H.J. Grabe, H.J. Freyberger, A. O. Hamm, M. Weippert, Inter-individual differences in heart rate variability are associated with inter-individual differences in empathy and alexithymia, *Front. Psychol* 9 (2018), <https://doi.org/10.3389/fpsyg.2018.00229>.
- [51] G. Park, J.F. Thayer, From the heart to the mind: cardiac vagal tone modulates top-down and bottom-up visual perception and attention to emotional stimuli, *Front. Psychol* 5 (2014) 1–8, <https://doi.org/10.3389/fpsyg.2014.00278>. May.
- [52] M. Zammuto, C. Ottaviani, F. Laghi, A. Lonigro, The heart in the mind: a systematic review and meta-analysis of the association between theory of mind and cardiac vagal tone, *Front. Physiol* (2021) 12, <https://doi.org/10.3389/fphys.2021.611609>.
- [53] A. Lischke, D. Lemke, J. Neubert, A.O. Hamm, M. Lotze, Inter-individual differences in heart rate variability are associated with inter-individual differences in mind-reading, *Sci. Rep* 7 (1) (2017) 11557, <https://doi.org/10.1038/s41598-017-11290-1>.
- [54] A. Todorov, C.Y. Olivola, R. Dotsch, P. Mende-Siedlecki, Social attributions from faces: determinants, consequences, accuracy, and functional significance, *Annu. Rev. Psychol* 66 (1) (2015) 519–545, <https://doi.org/10.1146/annurev-psych-113011-143831>.
- [55] A. Bagnis, C. Ottaviani, K. Mattarozzi, Face your heart: resting vagally mediated heart rate variability shapes social attributions from facial appearance, *Curr. Psychol* (2023), <https://doi.org/10.1007/s12144-023-04339-0>.
- [56] M. Eckstein, I. Mamaev, B. Ditzen, U. Sailer, Calming effects of touch in human, animal, and robotic interaction—scientific state-of-the-art and technical advances, *Front. Psych* (2020) 11, <https://doi.org/10.3389/fpsyg.2020.555058>.
- [57] G.G. Berntson, J. Thomas Bigger, D.L. Eckberg, P. Grossmann, P.G. Kaufmann, M. Malik, H.N. Nagaraja, S.W. Porges, J.P. Sauk, P.H. Stone, M.W. Van Der Molen, Heart rate variability: origins, methods, and interpretive caveats, *Psychophysiology* 34 (6) (1997) 623–648, <https://doi.org/10.1111/j.1469-8986.1997.tb02140.x>.
- [58] T.W. Smith, C. Deits-Lebehn, P.G. Williams, B.R. Baucom, B.N. Uchino, Toward a social psychophysiology of vagally mediated heart rate variability: concepts and methods in self-regulation, emotion, and interpersonal processes, *Soc. Personal Psychol. Compass* 14 (3) (2020) e12516.
- [59] D.S. Quintana, A.J. Guastella, T. Outhred, I.B. Hickie, A.H. Kemp, Heart rate variability is associated with emotion recognition: Direct evidence for a relationship between the autonomic nervous system and social cognition, *Int. J. Psychophysiol* 86 (2) (2012) 168–172, <https://doi.org/10.1016/j.ijpsycho.2012.08.012>.
- [60] C.L. Craig, A.L. Marshall, M. Sjöström, A.E. Bauman, M.L. Booth, B.E. Ainsworth, M. Pratt, U. Ekelund, A. Yngve, J.F. Sallis, P. Oja, International physical activity questionnaire: 12-country reliability and validity, *Med. Sci. Sports Exerc* 35 (8) (2003) 1381–1395, <https://doi.org/10.1249/01.MSS.0000078924.61453.FB>.
- [61] C. Forde, A. Loy, S. O'Dea, F. Mulcahy, J. Gormley, C. Daly, Physical activity is associated with metabolic health in men living with HIV, *AIDS Behav* 22 (6) (2018) 1965–1971, <https://doi.org/10.1007/s10461-017-1715-8>.
- [62] J. Jennings, T. Kamarack, C. Stewart, M. Eddy, P. Johnson, Alternative cardiovascular baseline assessment techniques: vanilla or resting baseline, *Psychophysiology* 29 (6) (1992) 742–750.
- [63] R. Tiwari, R. Kumar, S. Malik, T. Raj, P. Kumar, Analysis of heart rate variability and implication of different factors on heart rate variability, *Curr. Cardiol. Rev* 17 (5) (2021), <https://doi.org/10.2174/1573403X16999201231203854>.
- [64] U. Sailer, R. Ackerley, Exposure shapes the perception of affective touch, *Dev. Cogn. Neurosci* 35 (2019) 109–114, <https://doi.org/10.1016/j.dcn.2017.07.008>. June 2017.
- [65] A. Manzotti, F. Cerritelli, J.E. Esteves, G. Lista, E. Lombardi, S. La Rocca, A. Gallace, F. McGlone, S.C. Walker, Dynamic touch reduces physiological arousal in preterm infants: a role for c-tactile afferents? *Dev. Cogn. Neurosci* (2019) 39, <https://doi.org/10.1016/j.dcn.2019.100703>.
- [66] I. Morrison, L.S. Löken, J. Minde, J. Wessberg, I. Perini, I. Nennesmo, H. Olausson, Reduced C-afferent fibre density affects perceived pleasantness and empathy for touch, *Brain* 134 (4) (2011) 1116–1126, <https://doi.org/10.1093/brain/awr011>.
- [67] P.E. Sifneos, The prevalence of 'alexithymic' characteristics in psychosomatic patients, *Psychother. Psychosom* 22 (2–6) (1973) 255–262, <https://doi.org/10.1159/000286529>.
- [68] S.C. Walker, A. Marshall, R. Pawling, Psychophysiology and motivated emotion: testing the affective touch hypothesis of C-tactile afferent function, *Curr. Opin. Behav. Sci* 43 (2022) 131–137, <https://doi.org/10.1016/j.cobeha.2021.10.004>.
- [69] D. Peyser, B. Scolnick, T. Hildebrandt, J.A. Taylor, Heart rate variability as a biomarker for anorexia nervosa: a review, *Europ. Eating Disorders Rev* 29 (1) (2021) 20–31.
- [70] R. Thapa, I. Pokorski, Z. Ambarchi, E. Thomas, M. Demayo, K. Boulton, A. J. Guastella, Heart rate variability in children with autism spectrum disorder and associations with medication and symptom severity, *Autism Res* 14 (1) (2021) 75–85.
- [71] R. Pawling, P.D. Trotter, F. McGlone, S.C. Walker, A positive touch: C-tactile afferent targeted skin stimulation carries an appetitive motivational value, *Biol Psychol* 129 (2017), <https://doi.org/10.1016/j.biopsycho.2017.08.057>.