

The influence of force on the encoding and perception of affective touch

Sophia Faresse¹ , Luidgi Thrace¹ , S. Hasan Ali² , Adarsh Makdani³ , Francis McGlone⁴, Andrew G. Marshall⁵ , Paula D. Trotter³  and Rochelle Ackerley¹ 

¹Aix Marseille Univ, CNRS, CRPN (Centre de Recherche en Psychologie et Neurosciences – UMR 7077), Marseille, France

²Institute of Population Health, Department of Psychological Sciences, University of Liverpool, Liverpool, UK

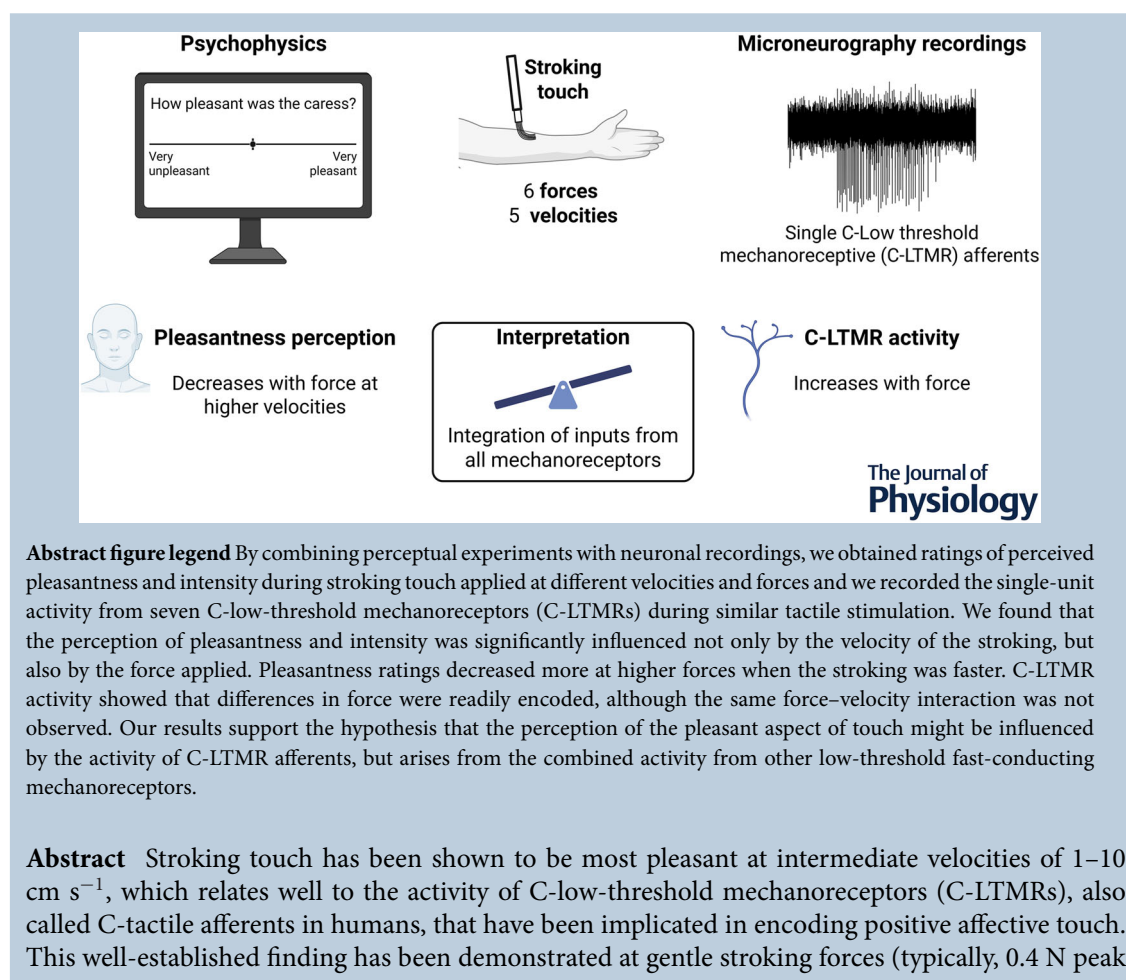
³Research Centre for Brain & Behaviour, School of Psychology, Liverpool John Moores University, Liverpool, UK

⁴Faculty of Science & Engineering, School of Life Sciences, Manchester Metropolitan University, Manchester, UK

⁵Institute of Life Course and Medicine Sciences, Pain Research Institute, University of Liverpool, Liverpool, UK

Handling Editors: Vaughan Macefield & Carole Torsney

The peer review history is available in the Supporting Information section of this article (<https://doi.org/10.1113/JP290946#support-information-section>).



S. Faresse and L. Thrace are joint first authors.

This article was first published as a preprint. Faresse S, Thrace L, Ali SH, Makdani A, McGlone F, Marshall AG, Trotter PD, Ackerley R. 2026. The influence of force on the encoding and perception of affective touch. bioRxiv. <https://doi.org/10.64898/2026.01.15.699730>.

© 2026 The Author(s). *The Journal of Physiology* published by John Wiley & Sons Ltd on behalf of The Physiological Society.

DOI: 10.1113/JP290946

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

normal force), yet few studies have investigated the effect of force on the perception of stroking touch or on the activity of C-LTMRs. We investigated the pleasantness and intensity of stroking touch (0.3, 1, 3, 10 and 30 cm s⁻¹) at different forces (0.2, 0.4, 0.8, 1.2, 1.6 and 2.0 N) on hairy forearm skin and compared this with responses from C-LTMRs during stroking touch at the same velocities, but over fewer forces (0.05, 0.4 and 1.5 N). We found significant effects of stroking velocity and force for both tactile pleasantness and intensity ratings. Pleasantness showed the typical inverted U-shaped relationship over stroking velocities, but this was modified by force; higher forces significantly decreased pleasantness at faster velocities. Conversely, tactile intensity increased linearly with both increasing velocity and force. Recordings from seven C-LTMRs showed that their firing frequency changed with stroking velocity, but that they were strongly modulated by force. Overall, we demonstrate the profound effect that force has on the perception of stroking touch, whereby tactile pleasantness and intensity appear to be a multi-faceted construct that is related to C-LTMR and A β -LTMR activity, respectively, but that the firing in individual mechanoreceptor populations cannot account fully for percepts.

(Received 16 January 2026; accepted after revision 30 August 2026; first published online 23 September 2026)

Corresponding author R. Ackerley: Centre de Recherche en Psychologie et Neurosciences (UMR 7077) CNRS – Aix-Marseille Université, 3 place Victor Hugo, Marseille 13003, France. Email: rochelle.ackerley@univ-amu.fr

Key points

- The skin is highly sensitive to small mechanical deformations, including dynamic touch and different forces.
- We obtained perceptual ratings for touch pleasantness and intensity over different stroking velocities and forces applied to the forearm. This was also compared with microneurography recordings from C-low-threshold mechanoreceptors (C-LTMRs).
- Building on previous work, we find that it is not only stroking velocity that affects pleasantness and intensity perception, but also stroking force. Pleasantness ratings decreased more at higher forces when the stroking was faster. C-LTMR firing showed that differences in force were readily encoded, although the same force–velocity interaction was not seen.
- This work expands the literature on affective touch to encompass the effects of force, which clearly modulates pleasantness.
- C-LTMR force and velocity information is likely to combine with information from all types of mechanoreceptors, including those from the fascia, to produce the resulting percept.

Introduction

Touch encoding begins in the skin, where low-threshold mechanoreceptors (LTMRs) located at the ends of afferent nerve fibres transmit specific components of mechanical signals to the CNS. Tactile perception is based upon

this input, combined with the contextual, cognitive and emotional state. LTMRs are all exquisitely sensitive to skin deformations and vary in type and density depending on the area of the body (Corniani & Saal, 2020; Vallbo & Johansson, 1984; Vallbo et al., 1995). The discriminative aspects of touch (e.g. knowing where, when and for

Sophia Faresse obtained her PhD in Neuroscience from Aix-Marseille University under the supervision of Rochelle Ackerley at the Centre for Research in Psychology and Neuroscience, where she is currently a postdoctoral researcher, investigating the physiology of touch by combining psychophysics and electrophysiology, with the goal of advancing innovation in the field of neuroprosthetics. **Luidgi Thrace** is currently a PhD student in Neuroscience at Aix-Marseille University under the supervision of Rochelle Ackerley. His PhD subject combines microneurography and massage to develop a computational model that assess and predict patterns of peripheral afferent firing to deep pressure touch.



how long) are encoded by fast-conducting $A\beta$ -LTMR fibres, whereas the positive affective (emotional) aspects of touch are believed to be reinforced by C-tactile (CT) afferents in humans, also known more generally as C-low-threshold mechanoreceptors (C-LTMRs) (McGlone et al., 2014; Schirmer, Croy et al., 2023). LTMRs all respond to low-force, dynamic touch, where microneurography studies in humans have shown how $A\beta$ -LTMRs encode various factors, such as indentation force and velocity (Knibestöl, 1973, 1975), stroking velocity (Edin et al., 1995; Essick & Edin, 1995) and dynamic force directionality (Birzniesis et al., 2001), mainly conducted on the glabrous, non-hairy skin of the hand. However, less is known about how forces are encoded and perceived in hairy skin, which is important to consider with respect to its role in receiving affective touch (McGlone et al., 2014; Schirmer, Croy et al., 2023).

Hairy skin has been investigated extensively on the forearm, in many different studies that have applied stroking stimuli at various speeds, focusing on the relationship between velocity and the pleasantness of touch. Initial work found that there was an inverted U-shaped relationship between stroking velocity and tactile pleasantness, where very slow and very fast speeds are rated as less pleasant (Essick et al., 1999). This was followed up by a microneurography study recording from C-LTMRs innervating the forearm that linked their firing with the perceived pleasantness of stroking touch (Löken et al., 2009). Here, the authors showed the tactile pleasantness of stroking followed an inverted U-shaped curve, where velocities between 1 and 10 cm s^{-1} were perceived as the most pleasant, which was shown to be related to the mean firing frequency of C-LTMRs. Furthermore, the authors also found a monotonic increase in the firing frequency of various $A\beta$ -LTMR fibres from 0.3 to 30 cm s^{-1} , reflecting that they encode increasing stroking velocity linearly. A similar study found the same results with regard to the relationships in C-LTMR firing at neutral temperature (akin to skin temperature) and also for $A\beta$ -LTMR hair follicle afferents (Ackerley, Wasling et al., 2014). A more recent study also found this inverted U-shaped relationship for C-LTMRs on the hairy skin of the leg (Löken et al., 2022). Two other investigations demonstrated the high sensitivity of $A\beta$ -LTMRs to stroking, where there was again an exponential increase in the firing of fast-adapting (FA) and slowly adapting (SA) $A\beta$ -LTMRs (Edin et al., 1995; Essick & Edin, 1995).

The relationship between the perception of tactile pleasantness and microneurography recordings has led to the affective touch hypothesis (Olausson et al., 2010; Vallbo et al., 2009), which postulates a dominant role for C-LTMRs in pleasant touch perception. This was followed by the social touch hypothesis (Morrison et al.,

2010; Olausson et al., 2010), which specifically implicated C-LTMRs in reinforcing human-to-human interactions. Many papers followed that have shown a clear relationship between stroking velocity and perceived pleasantness, where the intermediate speeds are more pleasant (e.g. Ackerley, Carlsson et al., 2014; Croy et al., 2021; Cruciani et al., 2021). However, there has been little consideration of how force influences C-LTMR firing and affective touch perception.

All the above microneurography studies investigating LTMR firing and stroking velocity have used a type of rotary tactile stimulator (RTS; Essick et al., 1999, 2010). This is typically calibrated to apply a maximum normal force of 0.4 N during stroking over the skin, and many psychophysical studies have also used this stroking force. Löken et al. (2009) tested two normal forces, namely 0.2 and 0.4 N, and no significant differences were found between these forces for the C-LTMR afferents, nor in the pleasantness ratings. Conversely, $A\beta$ -LTMR firing frequencies have been found to increase with force for some SA and FA $A\beta$ -LTMRs afferents, although the forces applied did not exceed 0.4 N (Edin et al., 1995; Essick & Edin, 1995; Löken et al., 2009). In terms of tactile perception, differences have been found in pleasantness with increasing force between textures, where soft, smooth textures (e.g. a brush) tend to have a constant level of pleasantness over different forces, whereas rougher, harder textures tend to decrease in pleasantness with increasing force (Cascio et al., 2008); however, the forces were not well controlled, because stroking was applied manually at light, medium or high forces. A further study using the RTS found that pleasantness generally decreased with stroking force, but this was less clear for soft, smooth textures, and the maximum force tested was 0.9 N (Essick et al., 2010). A more recent study explored the effect of more intense forces on stroking touch, testing the typical range of stroking velocities (0.3–30 cm s^{-1}) at RTS-set forces of 0.05, 0.4 and 1.5 N (Ali et al., 2023). They found that for all velocities, touch was perceived as more pleasant at 0.4 N compared with 0.05 and 1.5 N, and 0.05 N was significantly more pleasant than 1.5 N. Taking all these into consideration, we were thus interested in testing a wider range of forces.

Touch is multi-faceted, and participants can easily rate various percepts other than pleasantness (Jönsson et al., 2015; Sailer et al., 2020; Schirmer, Cham et al., 2023). One other relatively common percept to measure in skin stroking studies is tactile intensity, which has generally been found to increase linearly over the typical range of velocities tested (Jönsson et al., 2015; Schirmer, Cham et al., 2023; Sehlstedt et al., 2016; Tricoli et al., 2013). Intensity appears to be related more to the firing of $A\beta$ -LTMRs, which increase their activity monotonically with stroking velocity.

We investigated how stroking force affects pleasantness and intensity perception over different stroking velocities (Experiment 1), in addition to relating this to the firing of C-LTMRs in a similar protocol (Experiment 2), because C-LTMR activity has been linked directly with pleasantness, and little is known about their force encoding. We hypothesised that perception would vary with both the force and the velocity, but that this would be in different ways for pleasantness and intensity. Furthermore, we hypothesised that C-LTMR activity would also be modulated directly by stroking velocity and force, where the typical inverted U-shape would be seen for velocity, but that firing frequency would increase monotonically with force, as has been shown for C-LTMR firing during short normal indentations with calibrated monofilaments (Middleton et al., 2022) and during stroking for other A β -LTMRs (Edin et al., 1995; Essick & Edin, 1995; Knibestöl, 1973, 1975; Löken et al., 2009).

Methods

Experiment 1: psychophysical study of the perception of stroking at different velocities and forces

Ethical approval and participants. The experiment was approved by the ethical committee Comité de Protection des Personnes Île-de-France X (no. 2023-A01990-45) and was conducted in accordance with the guidelines set out in the *Declaration of Helsinki* (1964) and its later amendments, apart from preregistration in a database. We recruited 21 adult participants (aged between 19 and 29 years old, six males) who participated in the experiment at the Centre for Research in Psychology and Neuroscience in Marseille (UMR 7077). Participants were recruited by mailing list and word of mouth.

Exclusion criteria included pregnancy, being placed under legal protection, inability to understand the information and consent, and having a self-reported disorder that could alter tactile sensitivity (e.g. diabetic neuropathy, skin condition, psychiatric or neurological disorders). Participants received verbal and written information prior to agreeing to participate, and they all gave written informed consent. They received a remuneration of 10 euros for their time.

Stroking stimuli. We used a rotary tactile stimulator (RTS; Dancer Design, UK) robot to apply stroking stimuli to the middle of the forearm (determined with a measuring tape between the wrist fold and cubital fossa), between the ventral and dorsal aspects, as aligned with the thumb (Fig. 1A), at controlled velocities and calibrated normal forces. We used a flat soft artist's brush that had a width of 3 cm for the hairs, with a density of ~ 1 cm. We applied five stroking velocities (0.3, 1, 3, 10 and 30 cm s $^{-1}$) over six forces (0.2, 0.4, 0.8, 1.2, 1.6 and 2 N). The stroking was always applied in a proximal-to-distal direction. The normal forces were calculated from a dynamic stroking force curve that was calibrated up to the maximum force. Force curves were saved for each stroking trial. Stroking velocities were applied in a pseudorandomised order, and each velocity–force combination was repeated three times. This gave a total of 90 applied stimuli, and the experiment was completed in 1 h.

Procedure. Participants were seated comfortably on a chair, in front of a computer screen. Their left forearm was secured using a vacuum cushion to prevent movement and keep the forearm in a fixed and comfortable position. In their right hand, they held a visual analog scale (VAS) slider device that was used to move a cursor on the screen

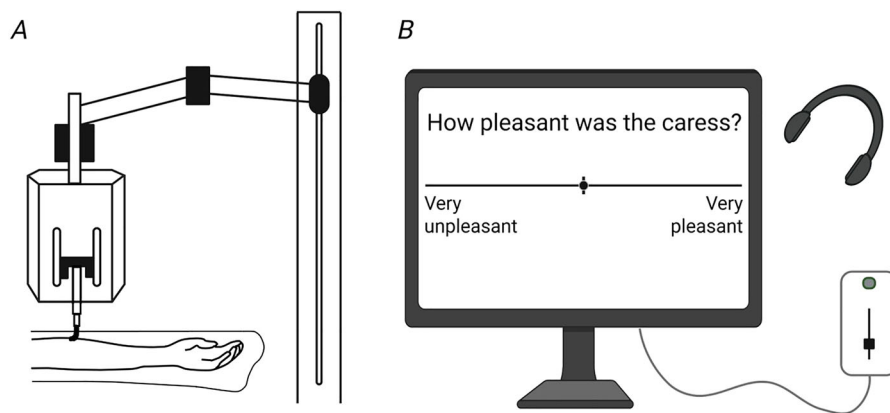


Figure 1. Diagram of Experiment 1 set-up

A, diagram of the rotary tactile stimulator robot. Stroking touch was applied to the middle of the left forearm. B, diagram of the slider device and the screen used to collect participants' ratings by moving the cursor displayed on the screen. A rating of pleasantness is shown as an example; the same design was used for intensity ratings ('How intense was the caress?' from 'very weak' to 'very strong').

to give tactile pleasantness and intensity ratings. A curtain was used to prevent the participant from seeing their forearm, and noise-cancelling headphones (Bose) were used to limit external sounds. The set-up is presented in Fig. 1. For each participant, the RTS was calibrated to apply the chosen forces before the experiment started. For the experiments, the participant was instructed to pay attention to the moving touch, then rate its pleasantness and intensity after each stroke, using two separate VASs displayed on a computer screen. After a stroking stimulus had terminated, the first VAS to rate tactile pleasantness appeared ('How pleasant was the caress?'), where the touch was rated from 'very unpleasant' (corresponding to -10) to 'very pleasant' (corresponding to $+10$) (Fig. 1). After they chose their response and clicked a button to enter it, a second scale appeared, where they rated the intensity of the touch ('How intense was the caress?') from 'very weak' (corresponding to -10) to 'very strong' (corresponding to $+10$). Once the second rating had been completed, the next stimulus was delivered.

Analysis. Preprocessing and visualisations of the data were conducted with Python (Jupyter Notebook, v.3.11.4 packaged by Anaconda). The statistical analyses were conducted in RStudio (R v.4.4.0), where linear and generalised linear mixed model analyses, in addition to regressions, were conducted with the lme4, lmerTest, glmmTMB and *post hoc* comparisons with the emmeans packages. According to previous literature, the decimal logarithm ($\log_{10}$) of the stroking velocity was used (Löken et al., 2009) to make the spacing between velocities equal. The α error was fixed at $P < 0.05$. Normal distribution of the residuals of the linear mixed models was assessed visually using histograms and Q-Q plots. Effect sizes were measured using partial eta squared (η_p^2). Ratings were analysed using separate linear mixed-effects models. The dependent variable was the pleasantness or intensity rating. Force, velocity and their interaction were included as fixed effects. The model included a random intercept for participant and a random slope for velocity across participants. Bonferroni-corrected *post hoc* tests were conducted to compare between stroking velocities and forces, and further contrast comparisons were used to investigate interaction effects between ratings of forces at each stroking velocity. A linear mixed model was also used in the analysis of the force recorded by the RTS. The dependent variable was the recorded force. Set force, velocity and their interaction were included as fixed effects. The model included a random intercept for participant. Bonferroni-corrected *post hoc* tests were conducted on RTS force data to compare between stroking velocity and set force, and for interactions, contrast comparisons were conducted for each force,

namely between the velocity of 30 cm s^{-1} (fastest), in comparison to all the other velocities.

Experiment 2: microneurography recordings from C-LTMR afferents to stroking at different velocities and forces

Ethical approval and participants. Experiment 2 was approved by the local ethical committee of Liverpool John Moores University (no. LJMU REC 14/NSP/039) in the UK and by the Comité de Protection des Personnes Sud-Ouest et Autre Mer III (no. 2021-A01604-37) in France. The research was conducted in accordance with the guidelines set out in the *Declaration of Helsinki* (1964) and its later amendments, apart from preregistration in a database for the UK. Typically, in microneurography studies studying single-unit cutaneous recordings from forearm hairy skin, the success rate is rather low and the data gained can be sparse. The data presented in the present study include recordings from five healthy adult participants [two females (20 and 39 years) and four males (20, 26 and 26 years)], for whom it was possible to run the full protocol on seven C-LTMRs. All participants received verbal and written information and signed an informed consent form.

Stroking stimuli. The set-up was a duplicate of that in Experiment 1, in which an RTS stroked over the forearm skin, depending on where the receptive field of a C-LTMR was found. The middle of the stroke was centred over the hotspot of the receptive field. The same five stroking velocities were used ($0.3, 1, 3, 10$ and 30 cm s^{-1}), although the forces tested were a little different, namely a very low force of 0.05 N (lower than the minimum 0.2 N used in Experiment 1), the typical 0.4 N (as in Experiment 1) and a higher force of 1.5 N (lower than the maximum 2.0 N used in Experiment 1). This was carried out for two reasons: (1) the forces corresponded to those used in an earlier psychophysical study, in which some of the microneurography was conducted in conjunction with Ali et al. (2023); and (2) fewer forces could be tested in microneurography owing to experimental constraints (e.g. duration of unit recordings, the application of higher forces could pull too much on the skin and disrupt the recording). Therefore, the lower force of 0.05 N was used as a minimal level to explore whether C-LTMRs responded to such low stroking forces, and the higher force allowed testing of a high force without compromising experimental stability. Furthermore, instead of a soft brush, a flat-bottomed probe covered by a soft polyurethane foam (stroking surface $\sim 10 \text{ cm} \times 2 \text{ cm}$) was used, as in the study by Ali et al. (2023). A comparison of the firing of C-LTMRs in previous work between a soft brush and a smooth

metal plate at skin temperature found a complete overlap of C-LTMR responses to these stroking velocities; therefore, we expected equivalence using a soft foam surface (Ackerley, Wasling et al., 2014; Löken et al., 2009; Watkins, 2022). The stimuli were applied in a pseudo-randomised order, and each velocity–force combination gave a total of 15 applied stimuli.

Procedure. The set-up was similar to Experiment 1, in that participants sat comfortably on a reclining chair with their left arm immobilised with a vacuum cushion. Perceptual ratings were not obtained during microneurography, as per previous experiments (Ackerley, Wasling et al., 2014; Löken et al., 2009), because the microneurography approach is already challenging, and the aim for Experiment 2 was to obtain electrophysiological recordings only. Peripheral nerve differential axonal recordings were made via microneurography (Ackerley & Watkins, 2022). An insulated high-impedance electrode (FHC, Bowdoin) was inserted into either the lateral antebrachial nerve ~3 cm proximal to the cubital fossa ($n = 54$ participants) or into the radial nerve at the upper arm ($n = 1$ participant) to record from the hairy skin of the lower arm. Neural signals were amplified, visualised and recorded using a NeuroAmpX connected to a PowerAmp with LabChart software (ADInstruments, Australia). Single LTMR units were identified via skin caressing, and C-LTMRs were classified according to Ackerley (2022), which included having a low threshold to indentation from a calibrated monofilament and high sensitivity to gentle stroking with a soft brush. Once a single C-LTMR of sufficient signal-to-noise ratio had been identified and characterised, the RTS was positioned perpendicularly over the middle of the receptive field, the chosen forces (0.05–1.5 N) were calibrated, and the protocol was applied.

Analysis. Microneurography data were analysed using LabChart (ADInstruments, Australia) and SpikeSort implemented in MATLAB (University of Gothenburg, Sweden). Single spike impulses were identified via a template-matching procedure and time stamped. Data analysis on the time-stamped spikes was performed using RStudio, according to the ratings and RTS force data. In brief, for the analysis of the microneurography C-LTMR mean frequencies, a generalised linear mixed model was used owing to the non-normal distribution of the data, where firing frequency was set as the dependant variable, stroking velocity and set force as fixed factors with their interaction, and each C-LTMR unit as a random factor, including a random intercept per unit. Bonferroni-corrected *post hoc* tests were conducted for force and for velocity.

Results

Experiment 1: psychophysical ratings of different stroking velocities and forces

Perceptual pleasantness ratings. Initially, we explored whether the relationship between tactile pleasantness and stroking velocity was best fitted by linear or quadratic regressions at each force. For all forces, there was a significant negative quadratic fit ($P < 0.001$ at 0.2, 0.4, 0.8, 1.2 and 1.6 N, and $P = 0.0226$ at 2 N) indicating an inverted U-shaped curve, but for the lower force curves from 0.2 to 1.2 N, a positive linear fit was also significant ($P = 0.00553$ at 0.2 N, $P = 0.00241$ at 0.4 N, $P < 0.001$ at 0.8 N, $P = 0.0310$ at 1.2 N, $P = 0.413$ at 1.6 N and $P = 0.278$ at 2 N). This can be seen in Fig. 2, where pleasantness increases for all forces during stroking at 0.3–1 cm s⁻¹. There is an overall peak in pleasantness around 3–10 cm s⁻¹ in the mean values over stroking velocities shown in Fig. 2B, yet this is clearly dependent on force, where forces over 1.2 N were much less pleasant, as seen in the pleasantness means over forces in Fig. 2C.

To investigate differences between the stroking velocities and forces, we applied a linear mixed model that revealed a significant effect of stroking velocity ($F_{4,34.87} = 10.95$, $P < 0.001$, $\eta_p^2 = 0.56$; Fig. 2B) and force ($F_{5,540.0} = 15.167$, $P < 0.001$, $\eta_p^2 = 0.12$; Fig. 2C) and a significant interaction between them ($F_{20,540.0} = 1.89$, $P = 0.0107$, $\eta_p^2 = 0.07$; Fig. 2A). For the effect of stroking velocity, Bonferroni-corrected *post hoc* comparison tests showed that pleasantness at 0.3 cm s⁻¹ was significantly lower than all the other velocities ($P < 0.001$ compared with 1 and 3 cm s⁻¹, $P = 0.00452$ compared with 10 cm s⁻¹), except 30 cm s⁻¹ ($P = 0.715$), and pleasantness at 30 cm s⁻¹ was significantly lower than at 10 ($P = 0.00303$) and 3 cm s⁻¹ ($P = 0.0107$; Fig. 2B). For force, mean pleasantness ratings were significantly higher for stroking at 2 N compared with 0.2, 0.4, 0.8 and 1.2 N (all $P < 0.001$) and 1.6 N ($P = 0.0124$). Mean pleasantness rating at 1.6 N was also significantly different from 0.4 ($P = 0.0204$) and 0.8 N ($P < 0.001$; Fig. 2C).

To investigate differences in the interaction between conditions, we conducted Bonferroni-corrected *post hoc* contrast tests that revealed significant decreases in pleasantness for higher stroking velocities at higher forces. Table 1 summarises these differences, showing that this effect starts at 3 cm s⁻¹ and becomes greater the faster the velocity. For 10 and 30 cm s⁻¹ stroking, there are numerous significant decreases for higher-force stroking (1.6 and 2.0 N), mainly showing differences between the intermediate forces of 0.8 and 1.2 N. Although no significant differences were found between the lowest forces and the intermediate forces, Fig. 2 and Table 1 indicate that the intermediate forces were the most pleasant.

Table 1. Significant differences in pleasantness ratings over forces per stroking velocity

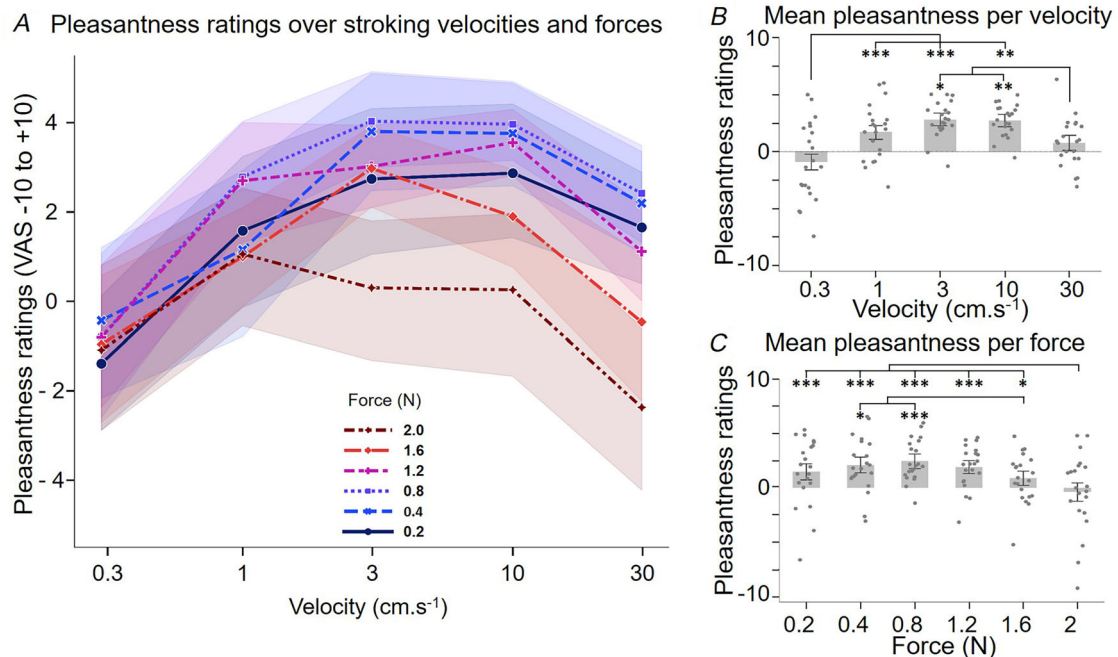
Velocity (cm s ⁻¹)	Significant differences in force comparisons per velocity
0.3	There were no significant differences between pleasantness ratings over forces; all <i>P</i> -values = 1.000
1	There were no significant differences between pleasantness ratings over forces; all <i>P</i> -values = 1.000, except for 0.4 compared with 0.8 (<i>P</i> = 0.778) and 1.2 N (<i>P</i> = 0.982), for 1.6 compared with 0.8 (<i>P</i> = 0.498) and 1.2 N (<i>P</i> = 0.638), and for 2 compared with 0.8 (<i>P</i> = 0.589) and 1.2 N (<i>P</i> = 0.751)
3	2.0 N was less pleasant than 0.4, 0.8 (both <i>P</i> < 0.001), 1.2 (<i>P</i> = 0.0187) and 1.6 N (<i>P</i> = 0.0221). All other <i>P</i> -values = 1.000, except for 2 compared with 0.2 N (<i>P</i> = 0.0562)
10	2.0 N was less pleasant than 0.2 (<i>P</i> = 0.0285), 0.4 and 0.8 (both <i>P</i> < 0.001) and 1.2 N (<i>P</i> = 0.00141). All other <i>P</i> -values = 1.000, except for 2 compared with 1.6 N (<i>P</i> = 0.752), and for 1.6 N compared with 0.4 (<i>P</i> = 0.402), 0.8 (<i>P</i> = 0.210) and 1.2 (<i>P</i> = 0.733)
30	1.6 N was less pleasant than 0.4 (<i>P</i> = 0.0234) and 0.8 N (<i>P</i> = 0.00946). 2.0 N was less pleasant than 0.4–1.2 N (all <i>P</i> < 0.001). All other <i>P</i> -values = 1.000, except for 2 compared with 1.6 N (<i>P</i> = 0.347), and 1.6 compared with 0.2 (<i>P</i> = 0.176) and 1.2 N (<i>P</i> = 0.900)

Pairwise contrasts per stroking velocity for pleasantness ratings, showing more significant differences between forces as velocity increased.

Perceptual intensity ratings. Next, we investigated tactile intensity perception and explored whether the velocity curves over the forces were best fitted by linear or quadratic regressions. For all the forces, significant positive linear regressions fitted the data (all *P* < 0.001),

as can be seen clearly in Fig. 3A, showing a monotonic increase in tactile intensity with stroking velocity and with force.

To investigate differences between the stroking velocities and forces, we used a linear mixed model

**Figure 2. Pleasantness ratings are influenced by the stroking velocity and applied force**

A, pleasantness ratings on a visual analog scale (VAS) ranging from -10 (very unpleasant) to +10 (very pleasant) over stroking velocities (x-axis) and forces (different lines), showing the means with $\pm 95\%$ confidence intervals. B, pleasantness ratings over velocities, averaged by force. Means with $\pm 95\%$ confidence intervals and individual participant ratings are shown. Significant differences between velocities were found at 0.3 cm s⁻¹, which was significantly less pleasant than all the other velocities, and at 30 cm s⁻¹, which was significantly lower than at 3 and 10 cm s⁻¹. C, pleasantness ratings over forces, averaged by velocity. Means with $\pm 95\%$ confidence intervals and individual participant ratings are shown. Significant decreases in pleasantness between 2.0 N and all other forces, apart from 1.6 N, were found, in addition to a significant decrease in pleasantness from 1.2 to 1.6 N. From *n* = 21 participants; **P* < 0.05, ***P* < 0.01 and ****P* < 0.001.

that showed a significant effect of stroking velocity ($F_{4,36.65} = 10.75$, $P < 0.001$, $\eta_p^2 = 0.54$; Fig. 3B) and force ($F_{5,539.45} = 534.77$, $P < 0.001$, $\eta_p^2 = 0.83$; Fig. 3C), with no significant interaction between these ($F_{20,539.45} = 1.07$, $P = 0.381$; Fig. 3A). In Fig. 3, which illustrates these effects, it is evident that participants were able to distinguish between all velocities and forces with respect to tactile intensity. For mean intensity over each velocity, Bonferroni-corrected *post hoc* tests showed that 0.3 cm s^{-1} was significantly lower than all other velocities (all $P < 0.001$; Fig. 3B). For force, all comparisons between all force levels were significantly different (all $P < 0.001$; Fig. 3C).

Comparisons of the peak normal forces delivered over different stroking velocities and forces. We analysed the recorded force output curves from the RTS during each stroking trial to explore whether the forces delivered matched the set forces, because this is rarely shown (cf. Edin et al., 1995; Essick et al., 2010), but is important to consider in the present work. We found that the RTS delivered a systematic underestimation of the set force, which became larger at the higher forces (Fig. 4). Figure 4A shows this underestimation for force, and Fig. 4B illustrates each force level. There was a

significant positive linear relationship for all the forces over the velocities (all $P < 0.001$, except for 0.4 N where $P = 0.00503$), apart from no relationship at 0.2 N ($P = 0.271$). A linear mixed model gave significant main effects of velocity ($F_{4,580} = 106.14$, $P < 0.001$, $\eta_p^2 = 0.42$) and set force ($F_{5,580} = 8465.98$, $P < 0.001$, $\eta_p^2 = 0.99$) that were extremely strong, and there was a significant interaction between them ($F_{20,580} = 15.5$, $P < 0.001$, $\eta_p^2 = 0.35$). Bonferroni-corrected *post hoc* tests showed that all set forces were significantly different (all $P < 0.001$) and all velocities were significantly different (all $P < 0.001$, except for 1 compared with 0.3 cm s^{-1} where $P = 0.0352$). To determine whether there were differences for each force level over increasing stroking velocity, we compared RTS output forces at 30 cm s^{-1} with the other velocities, for each set force. No significant differences were found between recorded normal forces applied at the 0.2 (all P -values = 1.000) and 0.4 N set forces ($P = 1.000$ compared with 10 cm s^{-1} , $P = 0.408$ compared with 3 cm s^{-1} , $P = 0.794$ compared with 1 cm s^{-1} , and $P = 0.202$ compared with 0.3 cm s^{-1}). At the set force of 0.8 N , the force delivered was significantly higher at 30 cm s^{-1} compared with 0.3 ($P = 0.00161$) and 1 cm s^{-1} ($P = 0.00668$) but not compared with 10 ($P = 1.000$) and 3 cm s^{-1} ($P = 0.336$). At the set force of 1.2 N , the force

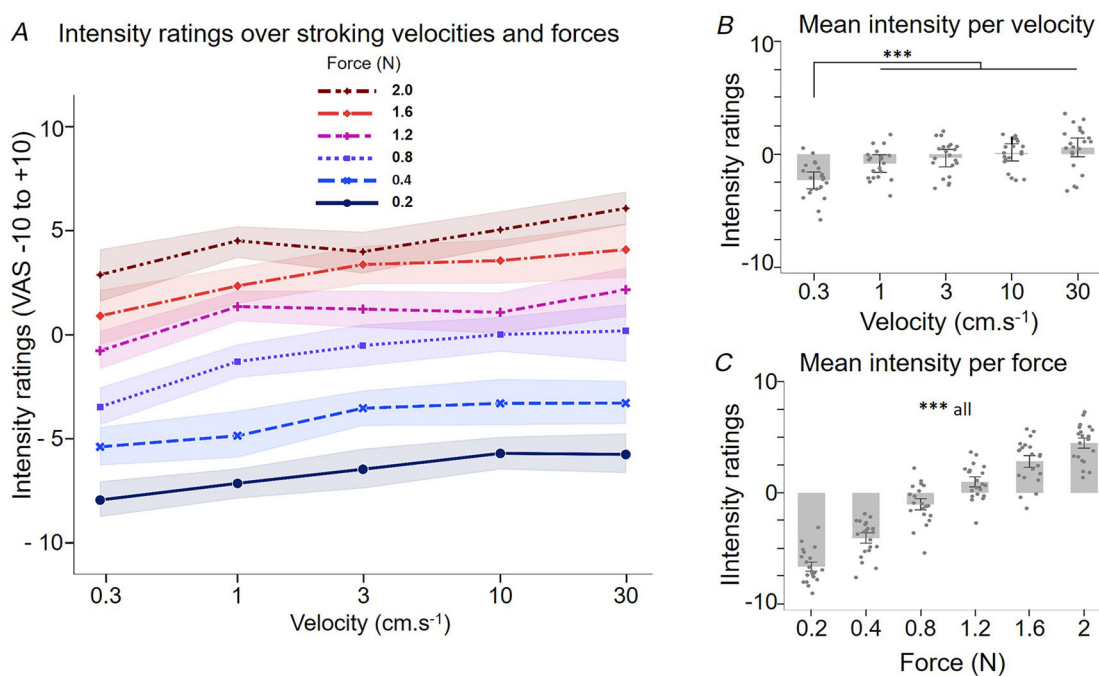


Figure 3. Intensity ratings are influenced by the stroking velocity and applied force

A, intensity ratings on a visual analog scale (VAS) ranging from -10 (very weak) to $+10$ (very strong) over stroking velocities (x-axis) and forces (different lines), showing the means with $\pm 95\%$ confidence intervals. B, intensity ratings over velocities, averaged by force. Means with $\pm 95\%$ confidence intervals and individual participant ratings are shown. Significant differences between velocities were found at 0.3 cm s^{-1} , which was significantly less intense than all the other velocities. C, intensity ratings over forces, averaged by velocity. Means with $\pm 95\%$ confidence intervals and individual participant ratings are shown. All comparisons were significantly different. From $n = 21$ participants, $***P < 0.001$.

delivered was significantly higher at 30 cm s^{-1} compared with all other velocities ($P < 0.001$ compared with 0.3 and 1 cm s^{-1} , and $P = 0.00141$ compared with 3 cm s^{-1}), apart from 10 cm s^{-1} ($P = 0.677$). At the highest set forces of 1.6 and 2.0 N , this effect was stronger, whereby there was a significant increase in delivered force at 30 cm s^{-1} , in comparison to all the other velocities (all $P < 0.001$).

Experiment 2: microneurography recordings of C-LTMR afferent responses to different stroking velocities and forces

Owing to the challenges of microneurography, a total of seven C-LTMRs were obtained for the full stroking protocol. We found that the mean firing frequency of C-LTMRs increased with increasing stroking velocity and force (Fig. 5). The C-LTMRs had mechanical indentation thresholds of $<0.005 \text{ N}$, and their locations are shown in Fig. 5B. Over the stroking velocities at 1.5 N , both significant positive linear ($P = 0.0104$) and negative quadratic ($P = 0.0215$) relationships were found, but there was no significant linear or quadratic relationship at 0.05 (linear, $P = 0.298$; quadratic, $P = 0.490$) or 0.4 N (linear, $P = 0.0539$; quadratic, $P = 0.898$). A generalised linear mixed model gave a significant main effect of stroking velocity [$\chi^2(4) = 10.29$, $P = 0.036$] and force [$\chi^2(2) = 15.76$, $P < 0.001$], but no significant interaction between these [$\chi^2(8) = 2.67$, $P = 0.953$]. Bonferroni-corrected *post hoc* tests showed that the velocity of 0.3 cm s^{-1} was significantly different from 10 and 30 cm s^{-1} ($P = 0.00970$ and $P = 0.00562$, respectively)

and that all force levels were significantly different (all $P < 0.001$, apart from 0.4 compared with 1.5 N , which was $P = 0.0115$).

Discussion

In the present study, we investigated the effects of stroking velocity and force on the perception of touch and related this to activity in C-LTMRs. Previous work has underscored the importance of stroking velocity in the perception of pleasantness, which has shown direct links to firing in C-LTMRs (Ackerley, Wasling et al., 2014; Löken et al., 2009), and we take this further by showing that force is an important factor in both tactile pleasantness and intensity evaluations, in addition to having a strong effect on C-LTMR activity. Both stroking velocity and force significantly influenced pleasantness and intensity ratings, although different effects were found for each. For pleasantness, the typical inverted U-shaped relationship was found for stroking velocities (Croy et al., 2021), and although a similar relationship was found for force, these two factors interacted to give significantly lower pleasantness when the stroke was fast and forceful. No effect of force was found during very slow stroking, but the effect became more pronounced the faster the stroke became. Intensity ratings followed clear linear relationships, where increases in both stroking velocity and force produced increased tactile intensity. The recordings from C-LTMRs highlight that neither the pleasantness nor intensity perceptual results mapped directly onto the activity of C-LTMRs, and we discuss the implications below.

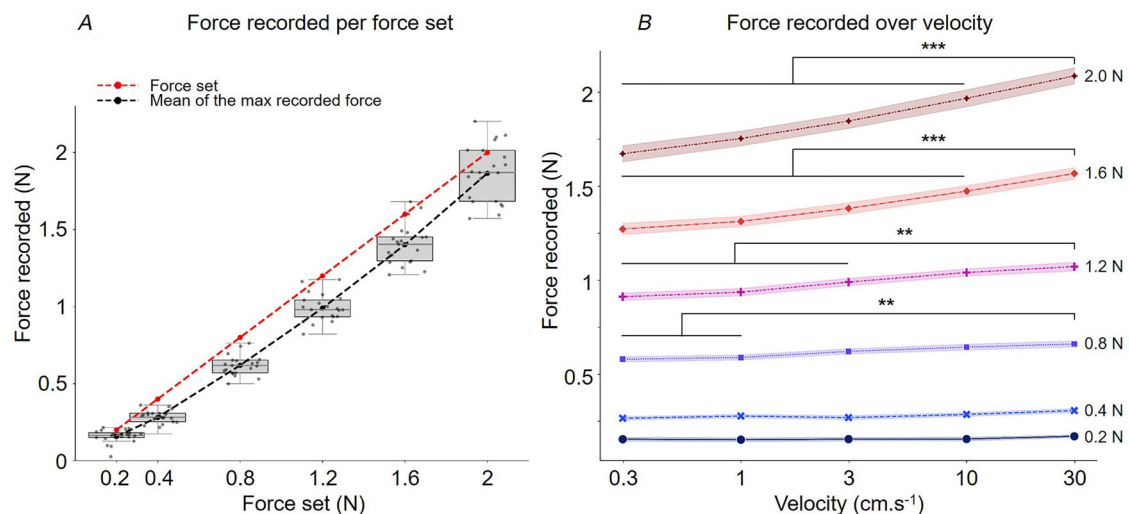


Figure 4. Comparisons of maximum normal forces delivered by the rotary tactile stimulator

In the psychophysical study, we recorded and analysed the maximum normal forces delivered by the rotary tactile stimulator. *A*, set forces (in red) and the peak normal forces obtained (in black, with box-and-whisker plots; $n = 21$ participants). *B*, peak normal forces obtained over the different velocities per set force, showing means with $\pm 95\%$ confidence intervals. ** $P < 0.01$ and *** $P < 0.001$.

Regarding the pleasantness findings, our results confirm the numerous studies that have shown an inverted U-shaped relationship between pleasantness and stroking velocity, with very slow and very fast velocities being slightly unpleasant and with a peak in pleasantness between 1 and 10 cm s^{-1} (Ackerley, Carlsson et al., 2014; Ackerley, Wasling et al., 2014; Croy et al., 2021; Essick et al., 1999; Löken et al., 2009). This is a relatively robust finding, although there is inherent variability in the ratings, and this relationship is not always found at an individual level, where many participants show positive linear curves as well (Croy et al., 2021). Stroking force has been little investigated in pleasantness perception, where the majority of studies have used a force of ~ 0.4 N, although this is only well controlled using a stroking robot. Löken et al. (2009) tested stroking forces of 0.2 and 0.4 N, but found no significant differences in terms of pleasantness or C-LTMR firing; however, the forces did not differ greatly, and only two were tested. Other studies have investigated different forces and textures, finding a general decrease in pleasantness with force, but it was less clear for smooth surfaces (Ali et al., 2023; Cascio et al., 2008; Essick et al., 2010). We extend these findings by investigating numerous stroking velocities and forces that were applied by a robot to show that even with brush stroking, pleasantness decreases with force, but only at faster stroking velocities. This implies that stroking velocity and force give related pleasantness percepts,

but that there is an interaction, potentially owing to the relative encoding by mechanoreceptors.

To complement the pleasantness ratings, we also investigated tactile intensity. In general, the literature shows that tactile intensity increases linearly with stroking velocity (Jönsson et al., 2015; Schirmer, Cham et al., 2023; Sehlstedt et al., 2016; Triscoli et al., 2013), as we found in the present study. Akin to pleasantness ratings, tactile intensity was also influenced by force, but increased linearly with it, and all comparisons between forces were significantly different. Similar results have been found previously between three forces, although no significant interaction was found between stroking velocity and force (Ali et al., 2023), which we found in the present study. The previous lack of interaction might have been attributable to fewer forces being tested, but in examining the present results, touch seemed to be much less intense at both lower velocities and forces. Again, this might be related to the underlying encoding via mechanoreceptors.

The literature on $A\beta$ -LTMRs shows that their firing frequency increases exponentially with stroking velocity (Ackerley, Wasling et al., 2014; Edin et al., 1995; Essick & Edin, 1995; Löken et al., 2009), but this relationship does not map directly onto pleasantness ratings (inverted U-shape) or intensity ratings (linear, with larger increases in the slope at lower velocities). This demonstrates how touch is a 'team effort', and the contributions of all types of sensory afferents can shape tactile perception (Saal &

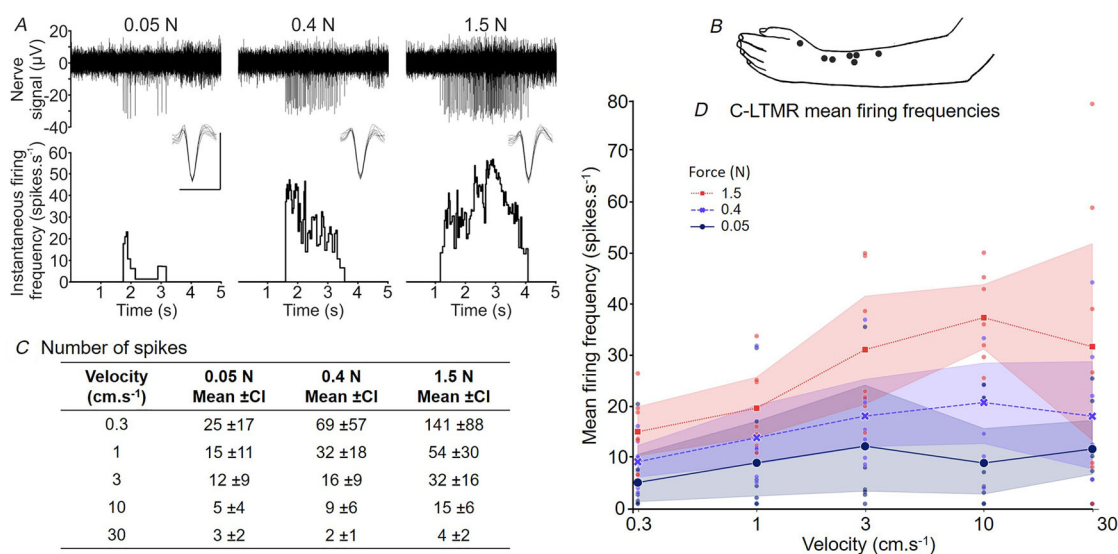


Figure 5. Firing frequencies of C-low-threshold mechanoreceptors over different stroking velocities and forces

A, examples of C-low-threshold mechanoreceptor (C-LTMR) firing and the instantaneous firing frequency for one unit stroked at 1 cm s^{-1} over 0.05, 0.4 and 1.5 N. The insets show an overlay of nine spikes from each trace, with the scale being 50 μV amplitude and 1 ms time. B, locations of the C-LTMR units. C, number of spikes found for each stroking velocity and force, giving the mean and 95% confidence intervals. D, mean firing frequency per stroking velocity at the forces of 0.05, 0.4 and 1.5 N (indicated by different lines and colours), with 95% confidence intervals as shading and smaller dots showing individual data points from $n = 7$ C-LTMRs.

Bensmaia, 2014). Nevertheless, it is of interest to relate the firing in different afferent populations to tactile percepts, and it can be seen that in general, tactile intensity is related to increases in firing frequency in $A\beta$ -LTMRs. When it comes to the contribution of C-LTMR afferents to tactile percepts, the relationships become more complex. C-LTMR input inherently arrives with a relative delay in the brain (timescale of seconds), in comparison to $A\beta$ -LTMR input (timescale of milliseconds), owing to their slower conduction velocity. C-LTMRs have been postulated to play a direct role in signalling the affective and emotional aspects of touch, owing to the relationship between their firing frequency and stroking velocity, which is correlated with pleasantness ratings (Ackerley, Wasling et al., 2014; Löken et al., 2009). However, the firing of C-LTMRs is not always significantly correlated with perceived pleasantness when additional parameters are manipulated, such as stroking at temperatures that are cooler or warmer than skin temperature, where both the C-LTMR firing and pleasantness perception diverge (Ackerley, Wasling et al., 2014).

Therefore, although C-LTMR activity has been implicated in pleasantness perception, this is a complex process that is also likely to depend on other afferent signals, in addition to central mechanisms (Case et al., 2023; Morrison, 2022; Schirmer, Croy et al., 2023; Vallbo et al., 2009). With regard to the encoding of force by C-LTMRs, few studies have investigated this; therefore, we provide new insights into the encoding of moving touch by C-LTMRs that are increasingly activated by force. It is unsurprising that no significant differences were found between stroking at 0.2 and 0.4 N by Löken et al. (2009), because these are both relatively low forces. In more recent work, it was clearly shown that C-LTMRs encode statically applied force, via calibrated monofilaments, from 0.004 to 0.1 N in a positive linear way (Middleton et al., 2022: supplementary figure 4B). However, the local forces produced from indentation are rather different from moving across the receptive field. Yet, we show that C-LTMRs encode different stroking forces well, possibly better than they encode stroking velocity.

Although we obtained recordings from a total of only seven C-LTMRs for the full protocol, the sample size is equivalent to other similar papers for LTMR recordings (Ackerley, Wasling et al., 2014; Löken et al., 2009, 2022), owing, in part, to the challenges of such micro-neurography experiments. Therefore, although further work should be conducted to explore dynamic force encoding in LTMRs further, the present results clearly demonstrate the capacity of C-LTMRs to signal force, although recordings from a wider range of forces would be ideal. Our results showed that C-LTMR firing increased to stroking velocities of 10 cm s^{-1} , but that the inverted U-shaped curve was not evident. This does correspond somewhat to the previous work, where

different mechanisms underlie the responses of C-LTMRs to each side of the stroking curve (Ackerley, 2022). At very slow velocities, C-LTMRs fire a lot, but their overall mean firing frequency is lower than at intermediate velocities (Ackerley et al., 2018; Löken et al., 2009). Conversely, C-LTMRs reach their limit of velocity encoding at 30 cm s^{-1} , where there is either no response or a few spikes; only when at least two spikes are present can a firing frequency be determined, hence the high variability seen in our results at 30 cm s^{-1} . The inverted U-shaped velocity tuning was not entirely present, but this was not unexpected (Ackerley, 2022), and the addition of more C-LTMRs could help to visualise this better, although the effect of stroking force dominated. C-LTMRs clearly fired much more to 1.5 N, in comparison to stroking at lower forces, yet we can ask whether pleasantness was directly related to this. Our perceptual results showed highest pleasantness for 0.2–0.8 N stroking, with no differences between these forces; therefore, the activity tuning to force in C-LTMRs is intriguing. However, this again underlies the idea that touch depends on all incoming inputs, from A- and C-fibre mechanoreceptive afferents to other afferents, such as thermoreceptors and nociceptors. Further work should investigate the effects of forces more on different $A\beta$ -LTMRs, because although $A\beta$ -LTMRs have been shown to encode force monotonically, it is possible that various types encode forces in different ways. It is also likely that at higher forces, C-mechanosensitive nociceptors start to contribute to perception. Studies have shown that C-mechanosensitive nociceptors can occasionally be activated via monofilament indentation from 0.0025 N and can fire occasionally in response to a brush stroke (Watkins et al., 2017). Therefore, with increasing force, these might be recruited more, and the balance is tipped from the C-LTMR-dominating positive affect to increased nociceptor negative affect, which should be investigated in further work.

In addition to the need to record from more afferents, further work could probe the effect that we found of increasing RTS applied force with increased stroking velocity. Overall, the recorded force was always less than the set force, and we found that this effect was more profound at slower stroking and higher forces. Few studies have looked at the output from the RTS, which is calibrated in terms of stroking direction, speed and force. However, the significant increase in delivered force in comparison to set normal force might have impacted the perception. It is difficult to quantify the exact impact in the present study; therefore, future work should take this into consideration, both mechanically and perceptually, when exploring interactions over the skin.

To conclude, our results call for a revision of the present models of affective touch perception, in which force is often not considered a central parameter. This relates well to more recent work investigating the pleasantness

of deep touch, which is an important aspect in affective and social touch, such as the impact of a hug or relaxation from a massage (Case et al., 2020, 2023). Both tactile pleasantness and intensity clearly relate to the firing of C-LTMR and A β -LTMR afferents, respectively, yet mounting evidence, combined with our present findings, demonstrate the complexity of affective touch perception and that it requires input from many different types of mechanoreceptors and other sensory afferents.

References

- Ackerley, R. (2022). C-tactile (CT) afferents: Evidence of their function from microneurography studies in humans. *Current Opinion in Behavioral Sciences*, **43**, 95–100.
- Ackerley, R., Carlsson, I., Wester, H., Olausson, H., & Backlund Wasling, H. & Backlund Wasling, H. (2014). Touch perceptions across skin sites: Differences between sensitivity, direction discrimination and pleasantness. *Frontiers in Behavioral Neuroscience*, **8**, 54.
- Ackerley, R., Backlund Wasling, H., Liljencrantz, J., Olausson, H., Johnson, R. D., & Wessberg, J. (2014). Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. *Journal of Neuroscience*, **34**(8), 2879–2883.
- Ackerley, R., & Watkins, R. H. (2022). Microneurography: Recordings from single neurons in human peripheral nerves. In N. Holmes (Ed.), *Somatosensory research methods*. Springer.
- Ackerley, R., Wiklund Fernström, K., Backlund Wasling, H., Watkins, R. H., Johnson, R. D., Vallbo, Å., & Wessberg, J. (2018). Differential effects of radiant and mechanically applied thermal stimuli on human C-tactile afferent firing patterns. *Journal of Neurophysiology*, **120**(4), 1885–1892.
- Ali, S. H., Makdani, A. D., Cordero, M. I., Paltoglou, A. E., Marshall, A. G., McFarquhar, M. J., McGlone, F. P., Walker, S. C., & Trotter, P. D. (2023). Hold me or stroke me? Individual differences in static and dynamic affective touch. *PLOS ONE*, **18**(5), e0281253.
- Birznieks, I., Jenmalm, P., Goodwin, A. W., & Johansson, R. S. (2001). Encoding of direction of fingertip forces by human tactile afferents. *Journal of Neuroscience*, **21**(20), 8222–8237.
- Cascio, C., McGlone, F., Folger, S., Tannan, V., Baranek, G., Pelphrey, K. A., & Essick, G. (2008). Tactile perception in adults with autism: A multidimensional psychophysical study. *Journal of Autism and Developmental Disorders*, **38**(1), 127–137.
- Case, L. K., Liljencrantz, J., McCall, M. V., Bradson, M., Necaie, A., Tubbs, J., Olausson, H., Wang, B., & Bushnell, M. C. (2020). Pleasant deep pressure: Expanding the social touch hypothesis. *Neuroscience*, **464**, 3–11.
- Case, L. K., Madian, N., McCall, M. V., Bradson, M. L., Liljencrantz, J., Goldstein, B., Alasha, V. J., & Zimmerman, M. S. (2023). A β -CT affective touch: Touch pleasantness ratings for gentle stroking and deep pressure exhibit dependence on A-fibers. *eNeuro*, **10**(5), ENEURO.0504.
- Corniani, G., & Saal, H. P. (2020). Tactile innervation densities across the whole body. *Journal of Neurophysiology*, **124**(4), 1229–1240.
- Croy, I., Bierling, A., Sailer, U., & Ackerley, R. (2021). Individual variability of pleasantness ratings to stroking touch over different velocities. *Neuroscience*, **464**, 33–43.
- Cruciani, G., Zanini, L., Russo, V., Boccardi, E., & Spitoni, G. F. (2021). Pleasantness ratings in response to affective touch across hairy and glabrous skin: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, **131**, 88–95.
- Edin, B. B., Essick, G. K., Trulsson, M., & Olsson, K. A. (1995). Receptor encoding of moving tactile stimuli in humans. I. Temporal pattern of discharge of individual low-threshold mechanoreceptors. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, **15**, 830–847.
- Essick, G., & Edin, B. (1995). Receptor encoding of moving tactile stimuli in humans. II. The mean response of individual low-threshold mechanoreceptors to motion across the receptive field. *The Journal of Neuroscience*, **15**(1), 848–864.
- Essick, G. K., James, A., & McGlone, F. P. (1999). Psychophysical assessment of the affective components of non-painful touch. *NeuroReport*, **10**(10), 2083–2087.
- Essick, G. K., McGlone, F., Dancer, C., Fabricant, D., Ragin, Y., Phillips, N., Jones, T., & Guest, S. (2010). Quantitative assessment of pleasant touch. *Neuroscience & Biobehavioral Reviews*, **34**(2), 192–203.
- Jönsson, E. H., Backlund Wasling, H., Wagnbeck, V., Dimitriadis, M., Georgiadis, J. R., Olausson, H., & Croy, I. (2015). Unmyelinated tactile cutaneous nerves signal erotic sensations. *Journal of Sexual Medicine*, **12**(6), 1338–1345.
- Knibestöl, M. (1973). Stimulus-response functions of rapidly adapting mechanoreceptors in the human glabrous skin area. *The Journal of Physiology*, **232**(3), 427–452.
- Knibestöl, M. (1975). Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *The Journal of Physiology*, **245**(1), 63–80.
- Löken, L. S., Wasling, H. B., Olausson, H., McGlone, F., & Wessberg, J. (2022). A topographical and physiological exploration of C-tactile afferents and their response to menthol and histamine. *Journal of Neurophysiology*, **127**, 463–473.
- Löken, L. S., Wessberg, J., Morrison, I., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience*, **12**, 547–548.
- McGlone, F., Wessberg, J., & Olausson, H. (2014). Discriminative and affective touch: Sensing and feeling. *Neuron*, **82**(4), 737–755.
- Middleton, S. J., Perini, I., Themistocleous, A. C., Weir, G. A., McCann, K., Barry, A. M., Marshall, A., Lee, M., Mayo, L. M., Bohic, M., Baskozos, G., Morrison, I., Löken, L. S., McIntyre, S., Nagi, S. S., Staud, R., Sehlstedt, I., Johnson, R. D., Wessberg, J., ... Bennett, D. L. (2022). Nav1.7 is required for normal C-low threshold mechanoreceptor function in humans and mice. *Brain*, **145**(10), 3637–3653.
- Morrison, I. (2022). Affective and discriminative touch: A reappraisal. *Current Opinion in Behavioral Sciences*, **43**, 145–151.
- Morrison, I., Löken, L. S., & Olausson, H. (2010). The skin as a social organ. *Experimental Brain Research*, **204**(3), 305–314.

- Olausson, H., Wessberg, J., Morrison, I., McGlone, F., & Vallbo, A. (2010). The neurophysiology of unmyelinated tactile afferents. *Neuroscience and Biobehavioral Reviews*, **34**(2), 185–191.
- Saal, H. P., & Bensmaia, S. J. (2014). Touch is a team effort: Interplay of submodalities in cutaneous sensibility. *Trends in Neurosciences*, **37**(12), 689–697.
- Sailer, U., Hausmann, M., & Croy, I. (2020). Pleasantness only? How sensory and affective attributes describe touch targeting C-tactile fibres. *Experimental Psychology*, **67**(4), 224.
- Schirmer, A., Cham, C., Lai, O., Le, T. S., & Ackerley, R. (2023). Stroking trajectory shapes velocity effects on pleasantness and other touch percepts. *Journal of Experimental Psychology: Human Perception and Performance*, **49**, 71–86.
- Schirmer, A., Croy, I., & Ackerley, R. (2023). What are C-tactile afferents and how do they relate to “affective touch”? *Neuroscience and Biobehavioral Reviews*, **151**, 105236.
- Sehlstedt, I., Ignell, H., Backlund Wasling, H., Ackerley, R., Olausson, H., & Croy, I. (2016). Gentle touch perception across the lifespan. *Psychology and Aging*, **31**(2), 176–184.
- Tricoli, C., Olausson, H., Sailer, U., Ignell, H., & Croy, I. (2013). CT-optimized skin stroking delivered by hand or robot is comparable. *Frontiers in Behavioral Neuroscience*, **7**, 208.
- Vallbo, A. B., Olausson, H., & Wessberg, J. (2009). Pleasant Touch. In L. Squire (Ed.), *Encyclopedia of neuroscience* (pp. 741–748). Elsevier. <https://www.elsevier.com/books/encyclopedia-of-neuroscience/squire/978-0-08-044617-2>
- Vallbo, A. B., & Johansson, R. S. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Human Neurobiology*, **3**, 3–14.
- Vallbo, A. B., Olausson, H., Wessberg, J., & Kakuda, N. (1995). Receptive field characteristics of tactile units with myelinated afferents in hairy skin of human subjects. *The Journal of Physiology*, **483**(3), 783–795.
- Watkins, R. H. (2022). Slow touch in non-human species: Translational research into the C-tactile (CT) afferent system. *Current Opinion in Behavioral Sciences*, **43**, 193–199.
- Watkins, R. H., Wessberg, J., Backlund Wasling, H., Dunham, J. P., Olausson, H., Johnson, R. D., & Ackerley, R. (2017). Optimal delineation of single C-tactile and C-nociceptive afferents in humans by latency slowing. *Journal of Neurophysiology*, **117**(4), 1608–1614.

Additional information

Data availability statement

Data and scripts for Experiment 1 are available via an OSF repository at: <https://osf.io/gxnyj>. Owing to the more sensitive nature of human microneurography recordings, the microneurography data can be accessed upon reasonable request.

Competing interests

All authors report no conflict of interest.

Author contributions

S.F., L.T. and R.A. designed, performed and analysed Experiment 1. For Experiment 2, P.D.T., A.G.M., A.M., S.H.A. and F.M. designed the study, A.M., A.G.M. and S.H.A. performed the study, A.M. and S.H.A. analysed the data, and P.D.T. supervised the study. S.F. drafted the first version of the manuscript with R.A. All authors approved the final version of the manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

Funding

S.F. was funded by the CNRS MITI program in a grant to R.A. and by the Fondation ARC. The study was funded by an Agence Nationale de la Recherche (ANR, France) grant ‘REMASS’ to R.A. in the CRCNS International call on Computational Neuroscience – NEUC 2024 collaboration. A.G.M. was funded by the Pain Relief Foundation. This work was supported by an Undergraduate Research and Knowledge Exchange Internship Scheme (URKEIS) award from Manchester Metropolitan University, for which S.H.A. was the research intern.

Acknowledgements

Open access publication funding provided by COUPERIN CY26.

Generative AI statement

No generative AI tools were used in the preparation of this manuscript.

Keywords

affective touch, C-low-threshold mechanoreceptor, C-tactile afferent, human, mechanoreceptor, microneurography

Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of the HTML view of the article. Supporting information files available:

Peer Review History