NeuroImage 265 (2023) 119811

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Velocity-tuning of somatosensory EEG predicts the pleasantness of gentle caress

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ABSTRACT

Numerous studies have established an inverted u-shaped effect between the velocity of a caress and its pleasantness and linked this effect to the C-tactile (CT) system considered central for physical and mental health. This study probed whether cortical somatosensory representations predict and explain the inverted u-shaped effect and addressed associated individual differences. Study participants ($N = 90$) rated the pleasantness of stroking at varying velocities while their electroencephalogram was being recorded. An analysis across all participants replicated a preference for intermediate velocities, while a cluster analysis discriminated individuals who preferred slow ($N = 43$) from those who preferred fast stroking ($N = 47$). In both groups, intermediate velocities maximized amplitudes of a somatosensory event-related potential referred to as sN400, in line with the average rating effect. By contrast, group differences emerged in how velocity modulated a late positive potential (LPP) and Rolandic power. Notably, both the sN400 and the velocity-tuning of LPP and Rolandic power predicted the participants' pleasantness ratings. Participants were more likely to prefer slow over fast stroking the better their LPP and Rolandic power differentiated between different velocities. Together, these results shed light on the complexity of tactile affect. They corroborate an average preference for intermediate velocities that relates to largely shared effects of CT-targeted touch on the activity of somatosensory cortex. Additionally, they identify individual differences as a function of how accurately somatosensory cortex represents the velocity of peripheral input and suggest these differences are relevant for the extent to which individuals pursue beneficial, CT-targeted touch.

1. Introduction

Although gentle physical contact between closely bonded individuals is ubiquitous across mankind, the frequency and value of such contact nevertheless varies. Moreover, variation from what may be considered the norm has been linked to mental and physical health outcomes (Dagnino-Subiabre, 2022; Keizer et al., 2022) and spurred research into individual differences (Croy et al., 2021; Sailer and Ackerley, 2019). Yet, insights into what causes individuals to differ remain limited. Here, we pursued such insights by adopting a data-driven approach to group individuals based on their affective responses to touch and asked whether and how central somatosensory processes predict differential affective outcomes for identified response groups.

Friendly or benign touch between individuals, henceforth referred to as affiliative touch, marks positive social interactions. It is more frequent, the closer the relationship between interactants (Schirmer et al., 2021; Sorokowska et al., 2021) and has been linked to both short and long-term benefits. In the short-term, affiliative touch serves as a socio-emotional regulator by biasing positive affect (Jakubiak, 2021) and pro-social attitudes (Crusco and Wetzel, 1984; Fisher et al., 1976; Schirmer et al., 2016). In the long-term, it helps the maintenance of important social relationships and promotes well-being (Jakubiak and Feeney, 2017) by, for example, enhancing stress resilience (Dagnino-Subiabre, 2022). Indeed, touch processing anomalies or being deprived of affiliative touch for extended periods of time are being considered relevant for a range of psychological problems including, for example, dysfunctional attachment, autism, and insomnia (Beltrán et al., 2020; Keizer et al., 2022; Masson et al., 2020; Van Puyvelde and Mairesse, 2022).

Lab-based research on affiliative touch has focused on gentle stroking and its peripheral and central processing. This focus has been motivated by the discovery of a special unmyelinated mechanoreceptor referred to as C-tactile (CT) afferent (Vallbo et al., 1993, 1999; Zotterman, 1939). Like myelinated mechanoreceptors, such as Aβ fibers, CTs respond to low force skin indentations and dynamically moving touch. Yet, they are special in that they prefer touch velocities between 1 to 10 cm/s over slower and faster stroking (Löken et al., 2009) and a touch temperature typical for skin-to-skin contact (Ackerley et al., 2014). Moreover, their firing rate was found to correlate with ratings of a touch's pleasantness, which among other things, inspired the idea that CT input to the brain supports emergent central representations of the value of affiliative touch reinforcing such touch in human interactions (McGlone et al., 2014; Olausson et al., 2008; Vallbo et al., 2009). Indeed, it inspired the proposal that Aβ fibers support discriminative touch, with which we identify and manipulate objects, whereas CTs support tactile affect or the pleasurable feelings from contact with conspecifics (McGlone et al., 2014).

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https://doi.org/10.1016/j.neuroimage.2022.119811.
Received 26 July 2022; Received in revised form 9 December 2022; Accepted 12 December 2022

Although research at the group level firmly established that CT-targeted stroking velocities elicit more positive affect than slower and faster velocities, a closer look at individual data points revealed much variation and raised the possibility of different perceptual touch phenotypes with potential relevance for well-being. To formally address this possibility, Croy and colleagues (Croy et al., 2021) re-examined five published data sets ($N = 127$) and observed that the velocity effect in a trial-based analysis of individual participants was significant only 57% of the time. Moreover, of those participants with a significant velocity effect, half showed a significant linear relation between velocity and pleasantness, while half showed a significant quadratic relation as established at the group level.

Stimulated by this research, we sought to further examine variability in the affective evaluation and neural processing of affiliative touch. Specifically, we were interested in whether individuals naturally cluster in how they value such touch and in whether there exist neural markers that predict cluster belonging. With respect to the latter point, we targeted measures of the electroencephalogram (EEG) including two early somatosensory markers—a negativity peaking around 400 ms following stimulus onset (sN400) and Rolandic rhythms over contralateral somatosensory cortex. Additionally, a mid-frontal late positive potential (LPP) was of interest.

In a recent study, gentle stroking elicited an sN400 response that depended on skin site and stroking velocity (Schirmer et al., 2022). For stimuli applied to the palm's glabrous skin, which has no or very few CTs (Watkins et al., 2020), faster stroking was associated with a larger sN400. By contrast, for stimuli applied to the hairy skin of the arm, which is densely innervated by CTs, the sN400 was largest for stroking velocities known to maximally excite CTs when compared with slower or faster stroking. Additionally, this latter modulation predicted the perceived pleasantness of the touch. Hence, the authors speculated that the sN400 indexes CT driven somatosensory processes (Schirmer et al., 2022), which could be relevant in explaining individual differences in the affective value of gentle stroking.

Apart from ERPs, the power of cortical alpha and beta rhythms, henceforth referred to as Rolandic power, has been long established as a marker of sensory processing (Adrian and Matthews, 1934; Berger, 1929). Touching and being touched effectively suppress Rolandic power over relevant somatosensory areas. Moreover, recent research found that stimuli with a faster velocity are associated with stronger blood-flow to somatosensory cortex (Case et al., 2016) and that, correspondingly, Rolandic power monotonically declines (Schirmer et al., 2022; Valenza et al., 2015). Importantly, unlike the sN400, velocity-dependent changes in Rolandic power compare between hairy and glabrous skin pointing to an independence of CT skin innervation. Indeed, their quick onset and monontonic velocity response pattern aligns with the activity of Aβ fibers instead (Löken et al., 2009).

Last, we wished to explore a mid-frontal LPP that has been documented by Ackerley and colleagues (Ackerley et al., 2013) and subsequently by other groups (Hagberg et al., 2019; Haggarty et al., 2020). Extending this work, a more recent study showed that, like pleasantness ratings, LPP amplitude depends on stroking velocity in an inverted u-shaped manner (Schirmer et al., 2022). Importantly, however, this effect showed irrespective of whether stroking targeted the palm or the arm and failed to predict a touch's perceived pleasantness. Thus, like Rolandic power, the LPP seems to dissociate from basic CT signaling. Instead, it may reflect late, higher-order processing of affiliative touch that contributes to subjective touch perception in combination with other processes (Schirmer et al., 2022). Indeed, the LPP could help explain inter-subject variability as such variability may be responsible for a lacking association between LPP amplitude and pleasantness at the group level.

In sum, our study aims were two-fold. First, we pursued inter-subject variability in the affective response to the velocity of gentle stroking as to determine whether such variability naturally clusters. Second, we sought to explore the neural correlates associated with gentle stroking as to elucidate potential biological mechanisms that explain inter-subject variability and associated affective response types. Towards these goals, we delivered a stroking stimulus to the forearm of research participants who rated that stimulus' perceived pleasantness. As done previously (Croy et al., 2021; Löken et al., 2009; Schirmer et al., 2022), we manipulated the velocity of stroking in five steps between 0.5 and 20 cm/s so as to manipulate tactile affect and associated CT vs Aβ excitation.

Based on earlier observations, we made the following predictions. With respect to the affective ratings, we expected an average preference for CT-targeted velocities and a minimum of two participant clusters that potentially deviate from the established inverted u-shaped response (Croy et al., 2021). With respect to the EEG, we expected that the identified participant clusters differentiate in one or more of the somatosensory markers of interest. For example, we speculated that individual differences in the velocity-pleasantness link may produce corresponding differences in how velocity modulates sN400 or LPP. Alternatively, we reasoned that different affective response types may differ as a function of early vs. late somatosensory responses or with respect to markers previously linked to CT vs. Aβ signaling. Indeed, we were open to a range of different EEG group effects as the current literature provided no basis for more specific predictions.

2. Methods

This research was approved by the Clinical Research Ethics Committee in Hong Kong. The data that support the findings of this study are available from the corresponding author upon reasonable request.

2.1. Participants

We recruited 92 participants for this study, two of whom were excluded from statistical analysis because noise in the EEG signal or technical problems resulted in less than 30 epochs in one or more conditions. The data of 60 participants has already been reported previously with a focus on overall group effects (Schirmer et al., 2022). Thirty participants were added to enable a meaningful pursuit of individual differences. The final sample comprised 45 men and 45 women with a mean age of 21 years (SD 2.5). All participants reported being right-handed and none reported suffering from a diagnosed mental or neurological disorder.

2.2. Stimuli and apparatus

The tactile stimuli were delivered using a custom-built and Matlab-controlled cable-driven robot capable of 3D motion. The robot entailed 8 motors that could move a touch stimulator in any direction with high spatio-temporal precision and accuracy. In keeping with previous research, the touch stimulus in this study was a soft cosmetic brush with a tip size of about half a centimeter. To enable temporal alignment between touch onset and the EEG, we weaved soft copper wires into the brush that connected with ESP32 Capacitive Touch Sensor pins. When the brush contacted skin, these pins sent a signal to the EEG data acquisition computer. The touch sensing pins also facilitated calibrating the touch device for a given participant. They enabled position read-outs for a planned stroking trajectory allowing us to adjust this trajectory to the surface curvature of the target skin area and ensuring a consistent brush force of about 0.3 N.

Stroking stimuli were directed at the left dorsal forearm. Although most studies in the field have probed linear trajectories, recent evidence suggests oval trajectories are more pleasant (Shirato et al., 2018) and more representative of actual touch interactions (Lo et al., 2021). We, therefore, opted for an oval rather than a linear trajectory. The set points for this trajectory were a ~15 cm circumference, a minor radius of ~1 cm and a major radius of ~3.22 cm. Small deviations from these set points were necessary due to variation in skin area curvature across participants. Strokes were delivered at five velocities including 0.5, 1, 3, 10 and 20 cm/s for a duration of 2.5 s. Because different velocities necessarily covered different distances across the skin, we adopted a number of control measures. Specifically, we adjusted the starting position of strokes such that motion along the oval was balanced across trials for a given velocity within participants. Thus, all velocities completed the full oval at least once across trials (for further details see Schirmer et al., 2022).

Please note that velocity manipulations are inherently confounded, forcing experimenters to accept condition differences in either travel distance or stimulus duration. Here, we opted for the former because the latter creates issues for the interpretation of ERPs as both the onset and offset of a stimulus elicit an ERP (Luck, 2014). For the velocities tested here, the onset response would have always coincided, while the offset response would have varied considerably.

2.3. Procedure

After completing an informed consent procedure, the participant was seated and the experimenter prepared her/him for the EEG recording. The participant then placed her/his left forearm onto a comfortable arm rest under the touch stimulator. A curtain precluded the participant from seeing the forearm and the touch device. Next, the participant received instructions via a computer monitor placed in front of her/him. The participant was asked to insert noise-canceling ear-phones into the ears, which presented a soft white noise meant to mask noise from the movement of the touch device. The experimenter operated the device and re-adjusted the white noise volume until the participant no longer heard the touch device.

The experiment comprised 300 trials across which the five stimulus velocities were presented with equal probability in pseudo-random order such that the same velocity would not be presented consecutively. This resulted in 60 trials per condition, which was established as suitable in terms of participant fatigue and EEG effects during pilot testing.

A trial began with a fixation cross lasting for 0.4 to 0.55 s coinciding with the downward motion of the touch stimulator. After the stimulator contacted the skin, it began moving along the oval trajectory for 2.5 s. During this time and the following one second, the fixation cross remained on the computer screen and was then replaced by a pleasantness rating scale. The participants now used their right arm to operate a mouse and to move a cursor to a position on a continuous scale that reflected the pleasantness associated with the touch. The scale endpoints were marked with very unpleasant on the left and with very pleasant on the right and scores coded within a range of -100 to 100. Following the participant's response, there was a short inter-trial interval during which the screen remained blank. The interval lasted for 1, 1.5 or 2 seconds, drawn from a uniform distribution. The experiment was divided into four blocks of 75 trials. Participants had a short break after every 30 trials and a five-minute break between blocks. Trials lasted about 6.5 seconds and an experimental session lasted about 50 minutes. The procedures are summarized in Fig. 1.

2.4. Electrophysiological recording and analysis

The EEG was recorded using 64 Ag/AgCl electrodes, which were located according to the extended 10–20 system of the American Clinical Neurophysiology Society (Acharya et al., 2016). CPz was used as the online reference. Electrode impedance was below 20 kΩ. The data were recorded at 500 Hz with an ANT EEGo system. Only an anti-aliasing filter was applied during data acquisition (i.e., sinc filter with a half-power cut-off at half the sampling rate).

EEG data were pre-processed with EEGLAB v14.1.1 (Delorme and Makeig, 2004) implemented in MATLAB. The data were down-sampled to 250 Hz, low-pass filtered at 30 Hz (7.5 Hz transition bandwidth, -6 dB cut-off) and high-pass filtered at 0.1 Hz (0.1 Hz transition bandwidth, -6 dB cut-off). Then the data were re-referenced to the channel average and epoched with a window from -1 to 1 s around each stimulus onset. Afterwards, the data were subjected to manual inspection where channels and epochs with non-typical artifacts caused, for example, by movements or drifting were rejected. The cleaned data were then high-pass filtered at 1 Hz and subsequently entered in an adaptive mixture independent component analysis (AMICA) (Palmer et al., 2011). The resulting independent component structure was applied to the original data with the 0.1 - 30 Hz filter setting. Components reflecting typical artifacts (i.e., horizontal and vertical eye movements and eye blinks) were removed and the data were back-projected from component space into EEG channel space. The data were subjected to another round of visual inspection during which residual artifacts were removed. A current source density transformation was applied using the CSD Toolbox (Kayser and Tenke, 2015). This served to enhance spatial separation of temporally overlapping signal components and to facilitate the detection of independent cortical sources (Kamarajan et al., 2015).

For the ERP analysis, we then conducted a baseline correction using mean voltages within a window between -200 and 0 ms from stimulus onset. Subsequently, trial data were averaged within subjects and conditions. For the time-frequency analysis, we subjected epochs ranging from -1 to 1 s to a continuous wavelet transformation with cycles ranging from 3 to 7 for frequencies from 5 to 28 Hz in steps of 1 Hz. This returned 153 time points ranging from -663 and 667 ms around stimulus onset. The wavelet transforms were then baseline corrected using a window from -500 to -100 ms and their power was obtained and averaged for each participant, condition, time point, and frequency. For statistical analysis, we divided Rolandic rhythms into α-1 (8–9.9 Hz), α-2 (10–11.9 Hz), β-1 (12–17.9 Hz), β-2 (18–20.9 Hz), β-3 (21–28 Hz) in line with earlier research (Ritter et al., 2009; Schirmer et al., 2022). This enabled us to detect potential frequency specific effects of touch on the power of somatosensory processes.

Ultimate trial numbers per condition averaged across participants ranged from 54 to 56 (participant-wise min = 37).

2.5. Statistical analysis

All analyses were conducted in R (R Core Team, 2015). As a first step, we conducted a cluster analysis as follows. Each participant's rating data entered a polynomial regression analysis with the trial-wise ratings as the dependent variable and the second-order polynomial of the common logarithm of velocity as the independent variable. Linear and quadratic terms were orthogonal. For further processing, we then used the obtained linear and quadratic terms because these terms helped us characterize the subject-specific relation between pleasantness and velocity. Both terms from all participants then entered the Silhouette procedure allowing us to estimate the optimal number of clusters in the data. This number together with the subject-wise linear and quadratic terms then entered a k-means clustering routine. The assignment of participants to clusters then formed the between subject variable in all remaining analyses.

The remaining analyses were conducted using the same channels, time windows, and statistical approaches as in our previous publication and were thus set apriori (Schirmer et al., 2022). All dependent measures were subjected to separate second-order polynomial regression analyses with cluster and the common logarithm of velocity as the independent variables (Löken et al., 2009). Again, linear and quadratic terms were orthogonal. For power only, frequency band was added as an additional variable. To facilitate the interpretation of linear and quadratic terms in the model, we normalized dependent and independent variables. Thus, beta's expressed change in terms of standard deviations. Moreover, the sign of the linear term (i.e., +/-) could be interpreted as showing a positive or negative relationship, while the sign of the quadratic term could be interpreted as showing a convex (u-shaped) or concave (inverted u-shaped) relationship. Note that normalizations are strictly cosmetic and have no impact on the actual significance of linear and quadratic terms. To account for the repeated measures nature of the velocity variable, we added a random effects term to the regression

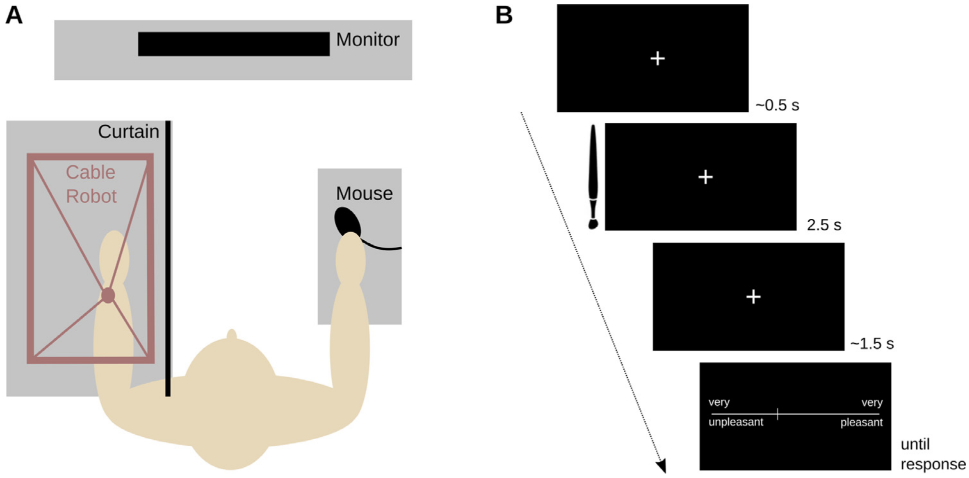

Fig. 1. Study procedures. A) Shown is the experimental set-up. B) Shown are the events making up a touch trial.

that specified slopes and intercepts for the rating analysis and intercepts only for the ERP and power analyses. As the latter relied on trial averages, they afforded no slope estimates. We implemented mixed models using the mixed function of the afex package (Singmann et al., 2019). F-statistics were obtained using the Satterthwaite approximation for degrees of freedom. Effect sizes were estimated with the eta_squared function of the effectsize package and are given as mean estimates with 90% confidence interval (Ben-Shachar et al., 2020).

3. Results

3.1. Pleasantness rating and participant clustering

As a first step, we checked whether we could replicate the inverted u-shaped effect reported in the literature. Thus, we subjected rating means to a mixed effects model with the second order polynomial of the common logarithm of velocity as the fixed effect and the participants' intercepts as the random effects. Slopes were not included because a corresponding trial-based model failed to converge. The simpler, converging model was significant (F[2, 358] = 3.35, p = .036, $p\eta^2$ = .0001 [0, 1]) and entailed a significant quadratic (beta = -1.75, SE = .67, t(358) = -2.58, p = .01) and a non-significant linear term (p = .866) indicating that intermediate velocities were, on average, most pleasant.

To better understand the present classification problem, we conducted a correlation analysis between subject-wise linear and quadratic terms. The result was significant (t(88) = 6.64, $p < .0001$, r = .58) indicating that a more positive linear term was associated with a more positive quadratic term. Expressed differently, participants who reported greater pleasantness with faster stroking were more likely to show a u-shaped rather than an inverted u-shaped relation between pleasantness and velocity.

The Silhouette procedure implied a solution with two clusters (average Silhouette score 0.49) as optimal such that we searched for two clusters in the k-means cluster analysis. The cluster results differentiated participants into those for whom both linear and quadratic term were on average negative and those for whom they were on average positive (Fig. 2). Cluster 1 included 43 participants (21 women), while cluster 2 included 47 participants (24 women). Together, these clusters explained 60% of the variance in the data.

Finally, we examined cluster differences in pleasantness ratings using a mixed effects model with cluster and the second order polynomial of the common logarithm of velocity as the fixed effects and the participants' slopes and intercepts as the random effects. This returned an effect of velocity (F[2,88] = 7.79, $p < .001$, $p\eta^2$ = .44 [.13, .62]), a marginal effect of cluster (F[2,88] = 3.37, p = .07, $p\eta^2$ = .38 [.00, .58]), and an interaction of velocity and cluster (F[2,88] = 93.89, $p < .0001$, $p\eta^2$ = .44 [.89, .99]). Separate analyses for each cluster indicated that the velocity effect was significant in both cluster 1 (F[2,42] = 62.6, $p < .0001$, $p\eta^2$ = .17 [.12, .21]) and 2 (F[2,46] = 40.16, $p < .0001$, $p\eta^2$ = .04 [.03, .06]). Yet, the nature of the effect differed. For cluster 1, both a negative linear (beta = -51.26, SE = 5.15, t(42) = -9.94, $p < .0001$) and a negative quadratic term (beta = -26.95, SE = 4.6, t(42) = -5.86, $p < .0001$) were significant. For cluster 2, both a positive linear (beta = 47.55, SE = 5.42, t(46) = 8.77, $p < .0001$) and a positive quadratic term (beta = 7.04, SE = 2.6, t(46) = 2.71, p = .009) were significant.

3.2. Cluster effects on neural processes

3.2.1. sN400

The sN400 results are illustrated in Fig. 3. Using a mixed modeling approach as detailed above, we asked whether the two clusters identified in the previous section explain variance associated with the sN400 response elicited to gentle stroking. The model returned the expected velocity main effect (F(2,356) = 31.63, $p < .0001$, $p\eta^2$ = .15 [.1, 1]) and an effect of cluster (F(1,88) = 3.9, p = .051, $p\eta^2$ = .04 [0, 1]). The interaction of cluster and velocity was non-significant (p = .408). Examination of the velocity effect showed that it was driven by a positive quadratic term of velocity on sN400 amplitude (beta = 4.8, SE = .605, t(356) = 7.93, $p < .0001$). The linear term was non-significant (p = .593). Irrespective of cluster, the sN400 amplitude was larger for intermediate when compared with slower and faster velocities.

Next, we probed whether the clusters differed in how their ERPs predicted pleasantness ratings. Thus, pleasantness was subjected to a mixed model with sN400 amplitude, cluster, and their interaction as fixed effects. We also added the second order polynomial of the common logarithm of velocity and its interactions as fixed effects to reduce the chance of false positive results. However, of interest was strictly the sN400 effect and its interaction with cluster. The participants' intercepts served as the random effect. The model returned a significant sN400 effect (F(1,424) = 10.52, $p < .0001$, $p\eta^2$ = .02 [.01, 1]), while other effects were non-significant ($ps > .201$). A larger (i.e., more negative) sN400 was associated with greater subjective pleasantness (beta = -.14, SE = .043, t(424) = -3.24, p = .001).

3.2.2. Rolandic power

Rolandic power analysis revealed a significant effect of velocity (F[2,2132] = 64.6, $p < .0001$, $p\eta^2$ = .06 [.04, .07]) and an interaction of velocity and cluster (F[2,2132] = 5.94, p = .003, $p\eta^2$ = .01 [.00, .01]). A separate analysis for cluster 1 was significant (F[2,1018] = 22.86, $p < .0001$, $p\eta^2$ = .04 [.02, .06]) indicating that power decreased linearly with increasing velocity (beta = -5.06, SE = .749, t(1018) = -6.75, $p < .0001$). The quadratic

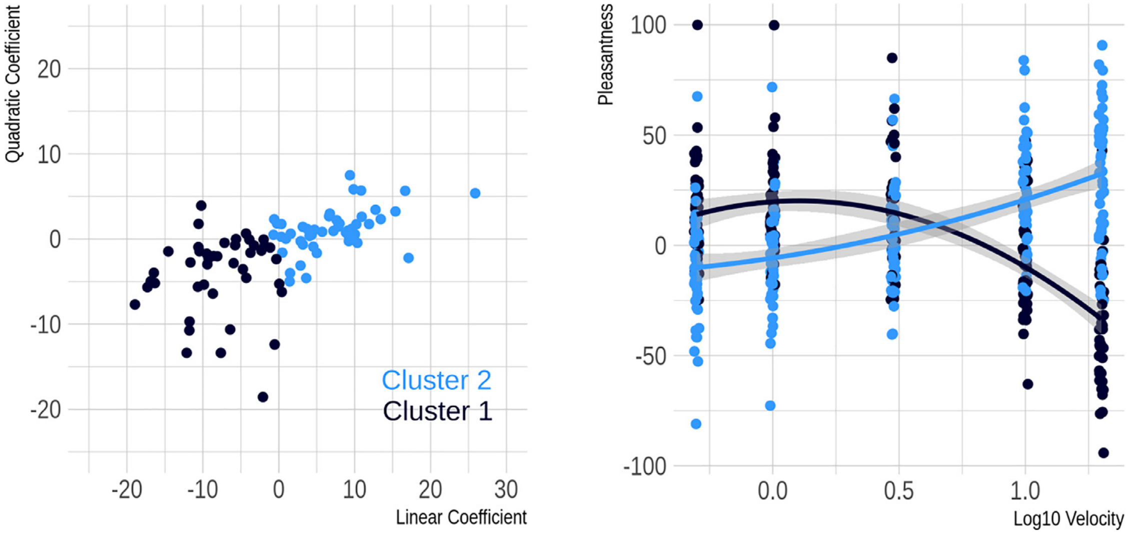

Fig. 2. Pleasantness ratings. Illustrated on the left are the subject-wise regression coefficients derived from regressing velocity against pleasantness ratings. The two blue colors highlight the two clusters obtained by k-means clustering. Illustrated on the right are the results from modeling the relationship between pleasantness and velocity. Each point represents the condition mean for one participant. The lines represent the fitted curve for each cluster.

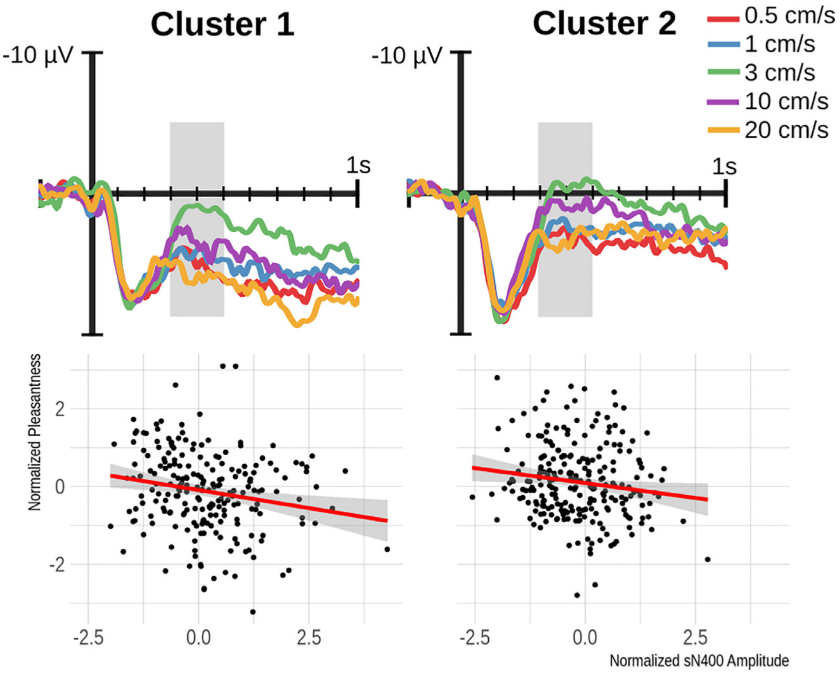

Fig. 3. ERP sN400 results. Illustrated in the top row are the grand average ERPs from the centroparietal electrodes contralateral to the stroking site that were used for statistical analysis. Illustrated in the bottom row are the normalized sN400 amplitudes for each subject and velocity plotted against pleasantness. The red lines show the linear fit between sN400 amplitude and the rated pleasantness of stroking. Effects were comparable across clusters.

coefficient was non-significant (p = .65). For cluster 2, we also found a significant effect of velocity (F[2,1114] = 49.25, $p < .0001$, pη^2 = .08 [.06, .11]). However, here this was due to both a linear (beta = -6.6, SE = .734, t(1114) = -8.98, $p < .0001$) and a quadratic effect (beta = -3.11, SE = .734, t(1114) = -4.23, $p < .0001$). Visual examination of the data illustrated in Fig. 4 shows that, whereas individuals in cluster 1 discriminated between the three slower velocities, individuals in cluster 2 did not. Indeed, excluding the faster velocities 10 and 20 cm/s from analysis preserved the velocity effect for cluster 1 (F[2,588] = 8.08, $p < .001$, pη^2 = .03 [.01, .05]) and eliminated this effect for cluster 2 (p = .84).

Again we pursued a potential relationship between power and subjective touch pleasantness. Specifically, we subjected pleasantness to a mixed model with power, cluster, frequency band, velocity and their interactions as fixed effects and the participants' intercepts as the random effect. Here, we were interested only in an effect of power and its interaction with cluster and frequency band. Other effects simply served to capture remaining variance and to reduce our type 1 error. The results were non-significant (*ps*>.278).

Last, we asked whether individuals for whom Rolandic power discriminates among slow stroking velocities are more likely to show negative linear and quadratic effects for the relation between stroking velocity and pleasantness ratings. Such an association is implied based on the cluster differences in Rolandic power as described above. To confirm this relationship, we conducted two regression analyses with the linear and the quadratic terms as the dependent variable, respectively. The independent variable was a slow stroking sensitivity score derived by subtracting the Rolandic power of the 1 cm/s condition from that of the 0.5 cm/s condition and that of the 3 cm/s condition from that of the 1 cm/s condition and taking the sum of both difference scores. The

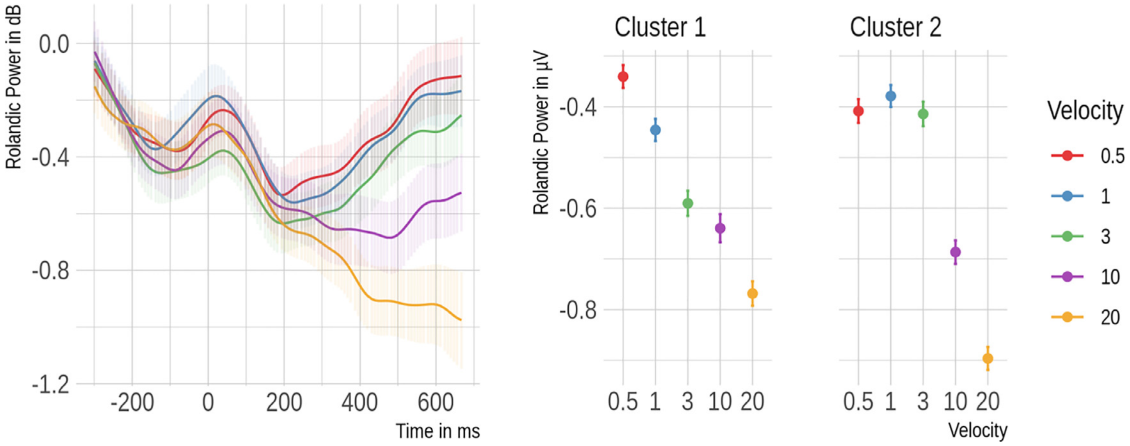

Fig. 4. Rolandic power changes elicited by gentle stroking. The left graph illustrates the time course of power changes time-locked to stimulus onset across all participants. Error bars reflect 95% confidence intervals. The two right graphs show for clusters 1 and 2 the mean power between 300 and 500 ms and 95% confidence intervals around the means.

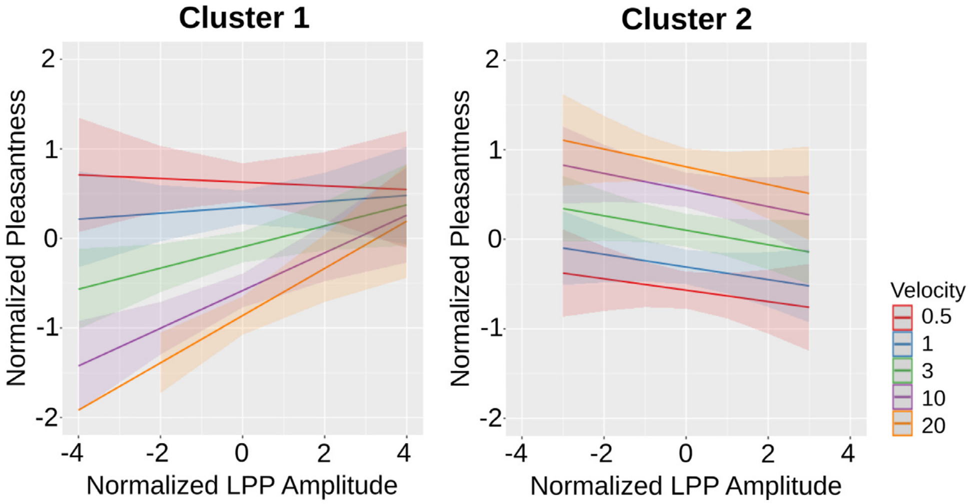

Fig. 5. Model fit of a linear mixed effect model with pleasantness as the dependent variable and LPP amplitude and log10 velocity as the fixed effects for clusters 1 and 2. The cluster 1 results entailed a significant interaction between the LPP and velocity.

larger this sum, the greater the linear decrease in power from slower to faster stroking and the more discriminating the somatosensory cortex response. Regression results approached significance for the linear term (beta = -2.72, SE = 1.6, t(88) = -1.68, *p* = .096) and were significant for the quadratic term (beta = -1.92, SE = .78, t(88) = -2.46, *p* = .016). Hence, greater Rolandic discrimination between slow stroking velocities positively predicted the typical inverted u-shaped effect of velocity on pleasantness.

3.2.3. *Fz late positive potential*

An analysis examining the effect of velocity and cluster on mean LPP amplitudes revealed a velocity main effect (F[2,356] = 11.59, *p* < .0001, $p\eta^2$ = .09 [.02, 1]). As expected, LPP amplitudes related to velocity in an inverted u-shaped manner (beta = -3.52, SE = .75, t(356) = -4.68, *p* < .0001). The linear relationship was non-significant (*p* = .352). The effect of cluster and the interaction of cluster and velocity were non-significant (*ps* > .612).

An analysis examining how LPP amplitudes together with cluster predict pleasantness yielded a significant interaction between the LPP, cluster, and velocity (F[1,367] = 4.11, *p* = .043, $p\eta^2$ = .01 [0, 1]; other *ps* > .175). A separate model for each cluster returned a significant LPP by velocity interaction for cluster 1 (F[1,176] = 7.08, *p* = .008, $p\eta^2$ = .04 [.1, 1]) but not for cluster 2 (*p* = .758). Exploration of the interaction in cluster 1 (Fig. 5) implied a positive relationship between LPP amplitude and pleasantness that was largest for the fastest velocity and systematically declined with slower stroking. Note, however, that separate linear regressions of LPP amplitudes against pleasantness were non-significant for all levels of velocity (*ps* > .1).

4. Discussion

Here, we pursued individual differences in the pleasure elicited by gentle stroking. Specifically, we asked whether individuals naturally divide into different affective response types and whether any divisions may be explained by the neural processes excited by somatosensory input. We measured affect in line with previous work by asking participants to rate the pleasantness of stroking varying in velocity. Additionally, we measured neural responses in the EEG focusing on three markers previously linked to gentle stroking. In what follows, we will detail rating and EEG results delineating two affective response types and showing that they differ in their cortical velocity tuning.

4.1. *Gentle stroking and subjective affect*

As expected, we found the velocity of stroking across the skin shapes subjective touch pleasantness and does so differently for different individuals. In line with earlier research, there was an average preference for intermediate stroking velocities that failed to show consistently at the individual level (Croy et al., 2021). Importantly, going beyond past efforts, we conducted a first data driven, statistical classification of touch pleasantness response types. This returned a correlation between linear and quadratic functions across participants indicating that, rather than being independent, both functions are naturally linked. Individuals with a negative quadratic relation between velocity and pleasantness were also likely to show a negative linear relation, while individuals with a positive quadratic relation were also likely to show a positive linear relation. Moreover, together quadratic and linear relations helped dissociate two groups that preferred slow and fast touch, respectively, and that were equally represented in the present sample and thus might be equally represented in the population at large. Whereas the slow group enjoyed slow and CT-targeted touch, the fast group favored faster touch that optimally excites Aβ fibers (Ackerley et al., 2018; Löken et al., 2009).

The manner in which we found stroking preferences divided suggests that both CT- and Aβ-targeted touch contributes to affect and could be relevant for bodily and social homeostasis. Indeed, natural tactile interactions may be geared towards addressing both somatosensory systems to similar degrees. In line with this, studies comparing the pleasantness of touch to the palm and arm, which drastically differ in CT innervation, found both to be similarly pleasurable (Schirmer and Gunter, 2017) and for average pleasantness ratings to show a comparable inverted u-shaped relation with velocity (Luong et al., 2017). Additionally, research measuring the physical properties of gently stroking a romantic partner revealed an average velocity of 10 cm/s (Lo et al., 2021; Strauss et al., 2020 mean not reported but likely ~15 cm/s). This value sits at the upper limit of what is considered CT optimal thus reflecting a natural tendency to move both slower and faster than the CT optimum perhaps so as to alternately bias either CT or Aβ signaling. Indeed, examining within toucher variation in velocity and other physical touch properties (e.g., spatial pattern, temporal rhythm) revealed such variation to be an important characteristic of socio-affectively motivated touch (Lo et al., 2021). Touchers were much more variable in their motion when they touched their partner or a dog than when they touched themselves or an object especially when intending to induce positive affect.

4.2. Neural responses to gentle stroking

Given that natural touch variably addresses CT and Aβ receptors, individuals may develop sensory processing specializations that explain their preferences for fast vs. slow touch. Here, we explored this possibility by measuring somatosensory signatures in the EEG including the sN400 and Rolandic power as markers for relatively early, stimulus-driven bottom-up representations of tactile input. Additionally, we used a mid-frontal LPP to measure later, perhaps more consciously driven top-down representations.

The sN400, a potential index of CT signaling, showed the expected inverted u-shaped relation with velocity as reported previously (Schirmer et al., 2022). Thus, as for the average rating results, intermediate velocities elicited, on average, the greatest sN400 amplitudes. Importantly, however, this pattern showed both for individuals preferring slow and fast touch. Moreover, across both groups, sN400 amplitude positively predicted rated pleasantness suggesting that its underlying processes are naturally relevant for affect, but perhaps in combination with other processes as discussed below.

Looking at Rolandic rhythms, we replicated earlier evidence of power decreasing with increasing velocity (Valenza et al., 2015). This agrees with insights from fMRI (Case et al., 2016) as well as with peripheral nerve recordings showing a monotonically positive relation between the firing of Aβ fibers and stroking velocity (Löken et al., 2009). Notably, the two touch clusters differed significantly in how velocity modulated Rolandic rhythms. Individuals who preferred slow stroking showed a negatively linear relationship between velocity and power, whereas individuals who preferred fast stroking showed both negatively linear and quadratic relationships. Thus, whereas the slow touch group significantly discriminated among slow velocities, the fast touch group did not. Indeed, the larger the discrimination among slow velocities in Rolandic power, the more likely seemed participants to show negative linear and quadratic relations between velocity and rated affect and to thus prefer slow stroking. Note, however, that only the quadratic relation was significant.

In addition to effects over somatosensory cortex, we also pursued a mid-frontal LPP (Ackerley et al., 2013; Hagberg et al., 2019; Haggarty et al., 2020; Schirmer et al., 2022). Like the sN400, this LPP showed an inverted u-shaped relation with velocity. Although it failed to differ between the two rating clusters, its relation with rated pleasantness differentiated clusters 1 and 2. In individuals who preferred slow touch, the LPP was clearly unrelated to pleasantness for the slowest touch but mounted a negative association as touch became faster. By contrast, individuals who preferred fast touch showed no association between LPP and rated pleasantness irrespective of whether touch was slow or fast. Thus, in slow but not fast touch people, more Aβ-targeted touch was more relevant for modulating the LPP and thus later evaluative processes that shape tactile affect. This aligns with the Rolandic rhythm results in that both suggest a preference for slow and CT-targeted touch arises with increased cortical velocity tuning.

Taken together, the present data link different neural processes, marked by different EEG/ERP signatures, to subjective pleasure and identify a complex, multi-faceted relationship. Importantly, they offer clues as to why some individuals prefer slow and others fast touch. Indeed, previous insights into the potential association between brain and peripheral processes make for two interesting implications. First, the fact that both affective response types showed the same sN400 effect, a proposed index of peripheral CT signaling (Schirmer et al., 2022), could mean that CT input drives cortical responses relatively uniformly. The maximal sN400 response to CT-targeted velocities could be a biological default that is perceptually vague, potentially preconscious, but nevertheless affectively positive (Olausson et al., 2002). Moreover, it could be instrumental in promoting the kind of CT-dependent experiences that maximize comfort and well-being. Second, group differences in the LPP and Rolandic power, two markers linked to Aβ signaling, point to individual variation in the manner in which Aβ input is represented in the brain. Moreover, the relation of these two markers to pleasantness accommodates the idea that Aβ representations provide the perceptual scaffolding that shapes conscious preferences for CT-targeted touch (Morrison, 2022; Schirmer and McGlone, 2022). Aβ input clearly contributes to and potentially overwrites more basic CT input to overt, self-reported tactile affect. Whether it also influences covert affect is an important question for future research.

The suspected importance of CT signaling for health and well-being has prompted research into the factors that shape preferences for CT-targeted touch. Both, genetic factors like those linked to autism and a person's tactile experiences as in the context of parental care or close relationships, have been raised as potentially relevant (Jackson et al., 2022; Keizer et al., 2022). Indeed, there is evidence that compared to neuro-typical individuals, individuals with autism spectrum disorder have, on average, a marginally weaker preference for slow vs. fast touch and fail to show a link between this preference and activity in the social brain (Perini et al., 2021). Additionally, there is evidence for a positive association between the frequency of self-reported affiliate touch and the inverted u-shaped relation between pleasantness ratings and stroking velocity (Sailer and Ackerley, 2019). Based on the present results, we speculate that both nature and nurture shape how the human cortex represents somatosensory input and, in this manner, determine what kind of touch individuals think they like. Moreover, we venture that a preference for slow vs. fast touch might also vary within individuals across time and reflect a perhaps temporary trade-off between the quality and quantity of available affiliative touch experiences.

4.3. Directions for future research

While the present study offers exciting new insights into the neural underpinnings of individual differences in the appreciation of gentle stroking, they also raise a number of questions for future research. A first question is whether and how tactile affect and central somatosensory representations differ with continued touch exposure. Available data indicate that, while subjective pleasure (Sailer et al., 2016), CT firing (Vallbo et al., 1999), and activity in somatosensory cortex (Sailer et al., 2016) decline with repeated stimulation, other aspects of tactile processing are retained or even intensified. For example, the initial CT firing burst (<150 ms) shows fairly consistently across stimuli (Vallbo et al., 1999). Additionally, activity in emotional brain regions (orbitofrontal cortex, putamen; Sailer et al., 2016) and associated heart rate responses (Triscoli et al., 2017) increase across time. How these patterns might dissociate between those who prefer fast and those who prefer slow touch awaits further research.

A second question concerns the role of somatosensory cortex in tactile affect. Past research has yielded conflicting results. A study by Case and colleagues (2016), for example, showed that transcranial magnetic modulation of primary somatosensory cortex impairs discriminative touch performance but not pleasantness ratings. However, other research including this present study could link affective responses to somatosensory activity (Morrison, 2016; Shirato et al., 2018). We speculate that sampling biases and individual differences explain this discrepancy and reason that future research needs to consider those. Indeed, it will be important to further examine the activity of somatosensory cortex as a function of touch preferences and to further delineate potential affective and discriminative representation.

Another interesting direction for future research is the specification of slow and fast touch preference types. As detailed above, stroking velocity has a negatively quadratic effect on CT firing and a positively quadratic effect on Aβ firing at the group level (Löken et al., 2009). Based on the present results, one might wish to explore whether these patterns hold when examining slow and fast touch individuals separately. Additionally, one might pursue the consequences of touch preferences for an individual's real-world touch exposure, social relationships, and well-being.

Finally, we wish to highlight the importance of studying touch experiences apart from those directed at CTs. Indeed, there are a range of affiliative touch actions including some that are less dynamic and have a stronger force than what is typical for a caress (Schirmer, Cham, et al., 2022). This includes, for example, squeezing, hugging and leaning, which may induce a deep pressure sensation that is also pleasurable and has potential health benefits (Case et al., 2020, 2021). Research suggests that such touch addresses primarily Aβ fibers (Case et al., 2021) and raises the possibility that CT and Aβ signaling convey complementary forms of human physical contact. Given the present results, it would be interesting to explore associated individual differences.

4. Conclusions

Although, on average, stroking feels most pleasant at intermediate velocities, individuals divide in whether they prefer it to be slow or fast. Those who prefer slow stroking show a negatively linear and quadratic relationship between velocity and pleasantness, whereas in those who prefer fast stroking, this relationship is positively linear and quadratic. Thus, the "typical" inverted u-shaped response represents individual touch preferences incompletely. Whereas slow and fast preference groups compare in an early somatosensory ERP, they differ in Rolandic power and in how a mid-frontal LPP relates to conscious tactile affect. Relationships between all three measures and subsequent pleasantness ratings show how complex conscious tactile affect is. Their compatibility with CT vs. Aβ signaling aligns with the idea that this affect results from vague and preconscious CT processes that are shared across individuals and scaffolded by more precise and conscious Aβ processes. Indeed, whether an individual overtly prefers slow or fast stroking relates to the nature of this scaffolding and to what extent it supports the cortical discrimination of stroking velocities. Together, these findings underscore the importance and usefulness of considering individual differences as we address questions about why we touch each other and how such touching "affects" us.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Credit authorship contribution statement

Annett Schirmer: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Oscar Lai:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Clare Cham:** Investigation, Writing – review & editing. **Clive Lo:** Investigation, Formal analysis, Writing – review & editing.

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