

EEG Captures Affective Touch: CT-Optimal Touch and Neural Oscillations

Mariana von Mohr¹, Michael J Crowley², Jessica Walthall², Linda C Mayes², Kevin A Pelphrey³,
& Helena JV Rutherford²

¹University College London, ²Yale Child Study Center, ³George Washington University

Correspondences to:
Helena JV Rutherford
Yale Child Study Center
Yale University
230 South Frontage Road
New Haven, CT, 06520
USA
Phone: 203-737-3408
Fax: 203-785-7926
Email: helena.rutherford@yale.edu

ABSTRACT

Tactile interactions are of developmental importance to social and emotional interactions across species. In beginning to understand the affective component of tactile stimulation, research has begun to elucidate the neural mechanisms that underscore slow, affective touch. Here, we extended this emerging body of work and examined whether affective touch (CT-optimal speed), as compared to non-affective touch (non CT-optimal speed) and no touch conditions, modulated EEG oscillations. We report an attenuation in alpha and beta activity to affective and non-affective touch relative to the no touch condition. Further, we found an attenuation in theta activity specific to the affective, as compared to the non-affective touch and no touch conditions. Similar to theta, we also observed an attenuation of beta oscillations during the affective touch condition, although only in parietal scalp sites. Decreased activity in theta and parietal-beta ranges may reflect attentional-emotional regulatory mechanisms; however, future work is needed to provide insight into the potential neural coupling between theta and beta and their specific role in encoding slow, tactile stimulation.

Key words: affective touch, CT fibers, EEG, neural oscillations

Introduction

Caress-like, gentle touch is important for social communication and the formation of social bonds (Hertenstein et al., 2006; Suvilehto, Glerean, Dunbar, Hari, & Nummenmaa, 2015). In rodents and primates, social gentle touch has long-term, stress-alleviating effects (Korosi & Baram, 2010), and reduces pain and separation distress (Agren, Lundeberg, Uvnas-Moberg, & Sato, 1995; Nelson & Panksepp, 1998). Similarly, gentle touch has positive effects in humans. Early in development, gentle touch helps calm infant pain and discomfort (Field, 2010) and acts as an important regulator of an infant's arousal in early parental interactions (Hofer, 1974). In adulthood, findings suggest that slow gentle touch modulates pain (Krahé, Drabek, Paloyelis, & Fotopoulou, 2016; Liljenkrantz et al., 2017) and autonomic arousal (Pawling, Cannon, McGlone, & Walker, 2017), while carrying positive affective valence (e.g., Pawling et al., 2017; Perini, Olausson, & Morrison, 2015). Consistent with the social touch as a stress buffer hypothesis (Morrison, 2016), these lines of research suggest that gentle touch exerts an influence on affective regulatory functioning throughout the lifespan. Moreover, clinical work suggests that tactile-based interventions improve clinical outcomes, including reduction of symptom severity in patients with rheumatoid arthritis and fibromyalgia, and reducing health complications in infants delivered pre-term (for reviews see Field, 2014; Hathaway et al., 2015). Given the likely regulatory function of gentle touch, there has been increasing interest in the mechanisms that may underpin the beneficial qualities of this type of touch.

Despite the mounting evidence for the impact of gentle touch on regulatory function and social bonds (Brauer et al., 2016; Field, 2010; Suvilehto et al., 2015), examination of tactile systems has been largely neglected in social neuroscience research. Importantly, emerging advances applying neurophysiological methods have begun to elucidate the affective component

of tactile stimulation (McGlone, Wessberg, & Olausson, 2014). This work targets specialised unmyelinated C tactile (CT) afferent fibers that are thought to primarily be stimulated by pleasant tactile sensations. Microneurography studies indicate that distinct from A β -mediated discriminative touch, unmyelinated CT afferents coding affective touch are located in hairy skin (Johansson & Valbo, 1979) and selectively respond to slow, gentle tactile stimulation (i.e., 1-10 cm/s). Selective CT stimulation is strongly correlated with reported pleasantness (Loken, Wessberg, McGlone, & Olausson, 2009) providing convergent evidence of the affective quality of gentle tactile stimulation. Recent work unpacking the neural pathways of CT afferents suggests their projection via thalamic pathways to brain regions implicated in emotion-related processing, social cognition, and interoception, including the insula cortex, dorsal anterior cingulate cortex, and orbitofrontal cortex (Bjornsdotter, Morrison, & Olausson, 2010; Craig, 2009; Gordon et al., 2011), with a recent study also implicating serotonin on the central processing of CT-targeted touch (Trotter et al., 2016). Engagement of emotion-relevant circuitry further supports the affective quality and rewarding properties of this type of touch.

The majority of studies examining the brain mechanisms for processing affective touch (i.e., slow, gentle tactile stimulation of hairy skin containing CT afferents) have employed functional magnetic resonance imaging (fMRI). fMRI research has shown the differential brain responses underlying affective touch for slow, CT-optimal speed on the forearm (hairy, CT skin) versus the palm (glabrous, non-CT skin) (Gordon et al., 2011), and affective touch for the forearm at slow, CT optimal speeds (i.e., 3 cm/s) versus fast, non-CT optimal speeds (i.e., 30 cm/s; Morrison, Bjornsdotter, & Olausson, 2011). fMRI provides good spatial resolution for identification of the brain regions modulated by affective touch, but relies upon changes in blood oxygenation levels (BOLD), which indirectly index changes in brain functioning. While BOLD

fMRI data correlates well with neural activity (Logothetis et al., 2001), it is not a direct measure of neural activity. In this regard, electroencephalography (EEG) constitutes a valuable complement to existing fMRI data by providing a direct correlate of neuronal activity, namely post-synaptic potentials of cortical pyramidal neurons, to elucidate more precisely the underlying neurophysiology of affective touch. Furthermore, EEG is widely employed across development, from newborns to older adults, conferring an advantage of providing a lifespan perspective on the assessment of the neural correlates of affective touch as this work continues.

Neural oscillations are a central focus of EEG research. Variation in cerebral integration across neural oscillations is thought to play a critical role in the emergence of actions, thoughts, emotions, and percepts (Cantero & Atienza, 2005; Nunez, 2000; Varela et al., 2001). Accordingly, EEG oscillations, defined by their frequency, magnitude, and phase, may underscore cognitive and affective processes reflecting the coordination of different brain systems, central to cerebral integration (Knyazev, 2007). In particular, EEG oscillations are traditionally subdivided into five frequency bands: delta (0.5-4 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), and gamma (30-80 Hz). The functional role of these fundamental frequencies is still debated, especially given the variation in contextual manipulations in which EEG is recorded (Knyazev, Savostyanov, & Levin, 2006). Nevertheless, there is growing agreement that low-frequency bands (e.g., delta and theta) may reflect activity of motivational and emotional systems; whereas higher frequency bands (e.g., alpha and beta) have been implicated more in inhibitory processes (Klimesch, 2012; Klimesch et al., 2007; Knyazev, 2007). For instance, if a task demands additional cortical processing and/or diverse processes, this may lead to alpha (and even beta) desynchronization, reflecting greater allocation of resources toward completion of that task (Knyazev, 2007; Knyazev, Savostyanov, & Levin, 2006; see also

Klimesch et al., 2007 for increased alpha synchronization in sites exerting top-down inhibitory control processes). In contrast, increased alpha activity has been noted in anticipatory periods preceding a sensory stimulus (Foxe et al, 1998), and in anxious participants, increased alpha has been associated with preparedness to process incoming sensory information (Knyazev, Savostyanov, & Levin, 2006). Notably, alpha and slow-wave oscillations (particularly theta) seem to be reciprocally connected: alpha activity seems to decrease while theta activity increases during activation; for example, during cognitive performance (and vice versa; Klimesch, 1999; Knyazev, 2007). Furthermore, enhanced theta power has consistently been observed during the processing of affectively-valenced cues (Aftanas et al., 2001, 2002, 2004; Balconi & Pozzoli, 2009; Krause et al., 2000), where decreases in alpha (and beta) are observed during relaxation (Diego et al., 2004; Field et al., 1996; Jacobs & Lunar, 1989; c.f. Aftanas & Golocheikine, 2001).

Only a handful of studies have begun to examine the relationship between EEG and the sense of touch. Preliminary research examining a single infant participant evidenced increased theta activity in response to an emotional stimulation, including pleasant forms of skin-to-skin contact (Maulsby, 1971). In advancing this work, it has been reported that tactile stimulation elicited by fabrics is associated with alpha/beta suppression particularly in regions covering somatosensory areas, possibly reflecting somatosensory processing (and hedonic valence effects in beta oscillations; Singh et al., 2014). Conversely, enhanced theta activity has been found in response to A β -discriminative touch (also accompanied by a decrease in alpha activity), with theta activity correlating with subjective ratings of stimulus intensity (Michail, Dresel, Witkovsky, Stankewitz, & Schulz, 2016). Finally, a frontal ultra-late potential evoked by slow CT stimulation has been observed, with such ultra-late potential modulating frontal theta, beta

(synchronization), and alpha (desynchronization) (Ackerley, Ericksson, & Wessberg, 2013). However, collectively, these studies have not provided a neural signature of affective touch and have not compared different forms of touch within-subjects. Although the initial evidence suggests EEG modulation in response to A β -discriminative touch and CT-optimal may overlap (e.g., increases in theta and decreases in alpha activity), this would be unexpected given the affective valence associated with slow, affective touch (Loken, Wessberg, McGlone, & Olausson, 2009; Pawling et al., 2017; Perini, Olausson, & Morrison, 2015), as well as its distinct neurophysiological pathway (McGlone et al., 2014).

In the present study, we examined the effects of affective touch (slow, at CT-optimal speed) versus non-affective touch (fast, at non CT-optimal speed) and rest (no tactile / touch stimulation) on neural oscillations (delta, 0.5-4 Hz; theta, 4-8 Hz; alpha, 8-13 Hz; beta, 13-30 Hz; and gamma, 30-80 Hz) across multiple scalp sites, to more precisely identify the neurophysiology of this critical regulatory function. Given literature suggesting alpha/beta suppression when processing tactile stimuli (Michail et al., 2016; Singh et al., 2014), we hypothesized that (1) affective and non-affective touch, relative to no touch, would decrease alpha and beta activity; (2) affective and non-affective touch would be associated with increased theta activity relative to the no touch condition, reflecting attention to involuntary salient sensory stimuli (e.g., Ianetti et al., 2008; Michail et al., 2016); and (3) tactile modulation of theta would be most prominent under the affective touch conditions, consistent with literature indicating that slow CT stimulation carries positive affective valence (Loken, Wessberg, McGlone, & Olausson, 2009; Pawling et al., 2017) and enhanced theta power has reliably been observed during the processing of affectively-valenced cues (Aftanas et al., 2001, 2002, 2004; Balconi & Pozzoli, 2009; Krause et al., 2000). Finally, although some studies suggest certain gamma modulation by

touch (e.g., Michail et al., 2016; and other sensory modalities, see Mouraux & Iannetti, 2009), no specific predictions were made with respect to delta or gamma oscillations.

Methods

Participants

Twenty-eight young adults (17 female; 11 male; M age 21 years; SD 2 years) were recruited from the local community. The Human Investigations Committee at Yale School of Medicine approved all procedures prior to recruitment and all participants provided informed consent.

Apparatus

Net Station 4.2.1 with a sampling rate of 250 Hz and high impedance amplifiers (Net Amps 200, 0.1 Hz high pass, 100 Hz low pass) were employed to record continuous EEG. A 128 Hydrocel Ag/AgCl electrode sensor net (Electrical Geodesics, Inc; (Tucker, 1993)) was placed on the participant's head and fitted according to manufacturer specifications. All electrodes were spaced evenly and symmetrically to cover the scalp from nasion toinion, and from left to right ear. Prior to application, the net was soaked in a warm potassium chloride solution to serve as the electrolyte. Electrodes were referenced to Cz during EEG recording and impedances were kept below 40 k Ω . Data was collected in a sound-attenuated room, with low ambient illumination.

Procedure

Prior to beginning the EEG visit, we measured and marked an 8 cm length on the participant's left forearm to identify the area to be brushed. This region was determined based on prior research that identifies this area when slowly brushed stimulates CT-afferents, with staff from those research studies training two research assistants to administer the brushing in the current study (Bennet et al., 2013; Gordon et al., 2011; Voos, Pelphrey, & Kaiser, 2013).

Continuous brush strokes were administered using a 6 cm watercolor brush back and forth within the marked region on the arm during the touch condition (affective or non-affective). Research staff were presented with a visual guide during each touch condition to facilitate consistency in the velocity of brushing in keeping with prior affective touch research (Bennet et al., 2013; Gordon et al., 2011; Voos, Pelphrey, & Kaiser, 2013). Prior to the paradigm beginning, participants all experienced being brushed at the different rates that were assessed in the task. During the affective touch condition, brush strokes were administered at the rate of 8 cm per second back and forth within the marked region. During the non-affective touch condition, brush strokes were administered at 32 cm per second back and forth within the same marked region. The velocity of the affective and non-affective touch was chosen as it has been shown to be optimal and non-optimal, respectively, for targeting CT afferents (Loken et al., 2009; Morrison et al., 2010); with these same velocities also used in previous studies (Bennet et al., 2013; Gordon et al., 2011; Voos et al., 2013).

There were 8 affective touch blocks and 8 non-affective touch blocks (order counterbalanced across participants). Each block contained 8 trials: A single trial consisted of 6 seconds of brush strokes (affective or non-affective depending on block, termed affective touch condition or non-affective touch condition, respectively), followed by 6 seconds of rest (recorded following the affective or non-affective touch, termed affective touch rest condition or non-affective touch rest condition, respectively). Rest conditions were first examined separately within each touch block (affective, non-affective) in case there were carry-over effects from the touch conditions to the rest conditions. Participants were instructed to have their eyes closed during the touch and rest within each block, but were asked to open their eyes between blocks (time between blocks was 12 seconds) to ensure they remained awake.

Data Analysis

Raw EEG data was pre-processed and prepared for statistical analysis using Net Station 4.5. Data was segmented into two-second epochs, creating 96 epochs per condition (affective touch, affective touch rest, non-affective touch, and non-affective touch rest). Artifact detection was $200\mu\text{V}$ for bad channels and ocular artifact removal (Gratton et al., 1983) using a blink slope threshold of $14\mu\text{V}/\text{ms}$ was applied to the EEG data. Eye blink and movement threshold was set to $150\mu\text{V}$. Spline interpolation was used to replace channels with artifacts in more than 40% of trials. EEG data were then re-referenced to the average reference of all electrodes and baseline-corrected using the average EEG recorded across the trial. Following pre-processing, there were on average 81 trials per condition (affective touch, affective touch rest, non-affective touch, non-affective touch rest).

Data was exported to Matlab 7.9.0 (R2009b MathWorks, Natick, MA) where Fast Fourier Transform analyses were performed. Average spectral power for delta (0.5–5Hz), theta (4–8Hz), alpha (8–13Hz), beta (13–30Hz) and gamma (30–80 Hz) frequencies were extracted by clusters from electrode sites in: prefrontal (Fp1, Fp2), frontal (F3, F4, F7, F8, Fz), central (C3, C4, Cz), parietal (P3, P4, Pz), temporal (T3, T4, T5, T6), and occipital (O1, O2) regions (consistent with the 10-20 electrode system; Jasper, 1958) (See Figure 1). A natural log-transform function (\ln) was conducted to normalize the data, and data points from one participant was removed as outlier following box-plot analysis (i.e., values were found $3\times\text{IQR}$ from above the third quartile or below the first quartile across multiple scalp sites, conditions, and frequency bands), resulting in a final sample of twenty-seven participants (16 female; 11 male; M age 21 years; SD 2 years).

Our data analytic plan first examined descriptive statistics followed by inferential statistics. Specifically, we conducted repeated measures ANOVAs specifying Condition

(affective touch, non-affective touch, non-tactile/rest) and Scalp Site (prefrontal, frontal, central, parietal, temporal, and occipital) on ln values for each frequency band. There was no a priori rationale that EEG recorded during the non-tactile (i.e., rest) conditions should differ when following the affective and non-affective touch tactile conditions, and therefore EEG were averaged across these conditions. Nevertheless, to validate this approach, we conducted repeated measures ANOVAs for each frequency band comparing spectral power by non-tactile conditions (i.e., rest following affective or non-affective stimulation as a function of scalp site). With the exception of delta, we found no main effect of non-tactile condition ($F's < 2.71$ $p's > .112$) and non-tactile condition did not interact with scalp site ($F's < 2.80$ $p's > .058$). We found a non-tactile condition by scalp site interaction when analyzing delta activity, $F(5,130)=2.74$, $p=.046$, $\eta^2_{\text{partial}}=.10$. Nevertheless, given that we found the same pattern of results on delta activity when including the two non-tactile/rest conditions (see supplementary materials) versus averaging the non-tactile/rest conditions on our inferential statistics, we present below the results for the analyses averaging across non-tactile/rest conditions on delta activity for consistency and clarity purposes. Effect size is presented as partial eta-squared (η^2_{partial}), where .01 represents a small effect size, .06 represents a medium effect size, and .14 represents a large effect size (Cohen, 1988). Greenhouse-Geisser corrections were used when sphericity assumptions were violated.

[Figure 1]

Results

Descriptive statistics

Average activity between the two rest conditions (affective touch rest, non-affective touch rest) was computed for each scalp site per frequency and employed as the baseline activity level for subsequent frequency band analyses involving the two touch conditions. In Table 1 we

present the log-transformed spectral power for delta, theta, alpha, beta, and gamma recorded from the rest, non-affective touch, and affective touch conditions across all scalp sites. We next examined the impact of touch (affective touch, non-affective touch, no touch during rest) employing a repeated-measures ANOVA specifying the within-subjects factors of experimental condition (rest, non-affective, affective touch) and scalp site (prefrontal, frontal, central, parietal, temporal, occipital) separately on delta, theta, alpha, beta, and gamma frequency bands. Results from these analyses, and follow-up pairwise comparisons conducted where appropriate, are presented below.

[Table 1]

Delta

Analyses on delta activity showed a main effect of scalp site, $F(5,130)=19.70$, $p<.001$, $\eta^2_{\text{partial}}=.43$. However, there was no main effect of condition, $F(2,52)=.26$, $p=.773$, $\eta^2_{\text{partial}}=.01$, and condition did not interact with scalp site, $F(10,260)=1.07$, $p=.376$, $\eta^2_{\text{partial}}=.04$. Together, these analyses suggest that affective and non-affective touch do not differentiate delta power from the rest (no touch) condition.

Theta

Analyses on theta activity showed that the main effects of condition, $F(2,52)=8.56$, $p=.001$, $\eta^2_{\text{partial}}=.25$, scalp site, $F(5,130)=5.71$, $p=.002$, $\eta^2_{\text{partial}}=.18$, and their interaction, $F(10,260)=5.54$, $p=.007$, $\eta^2_{\text{partial}}=.18$, were statistically significant. Therefore, we repeated the ANOVA including only the within-subjects factor of condition (rest, non-affective, affective touch) at each scalp site. The main effect of condition was statistically significant across all scalp sites, including prefrontal, $F(2,52)=6.71$, $p=.003$, $\eta^2_{\text{partial}}=.21$, frontal, $F(2,52)=6.22$, $p=.007$, $\eta^2_{\text{partial}}=.19$, central, $F(2,52)=4.64$, $p=.035$, $\eta^2_{\text{partial}}=.15$, parietal, $F(2,52)=9.33$, $p=.003$, $\eta^2_{\text{partial}}=.26$,

temporal, $F(2,52)=5.83$, $p=.010$, $\eta^2_{\text{partial}}=.18$, and occipital, $F(2,52)=5.57$, $p=.014$, $\eta^2_{\text{partial}}=.18$, scalp sites. As shown in Table 2, post-hoc pairwise comparisons with Bonferroni correction evidenced lower theta activity in the affective touch, as compared to the non-affective touch, condition across all scalp sites – except for a trend towards statistical significance in central regions ($p=.052$). Given that affective touch decreased theta activity relative to non-affective touch, we next examined whether there were any differences between the affective touch condition and the rest (no touch) condition at each scalp site (Table 2). We found lower theta activity in the affective touch, as compared to the rest condition, in frontal, central, parietal, and temporal scalp sites (and a trend towards statistical significance in prefrontal regions). In contrast, there was no statistically significant difference in theta activity between the non-affective touch and rest conditions across any scalp site. Taken together, these results suggest that affective touch, as compared to non-affective touch and rest conditions, may decrease theta activity across multiple scalp sites.

[Table 2]

Alpha

Analyses on alpha activity showed that the main effects of condition, $F(2,52)=4.23$, $p=.031$, $\eta^2_{\text{partial}}=.14$, scalp site, $F(5,130)=28.69$, $p<.001$, $\eta^2_{\text{partial}}=.53$, and their interaction, $F(10,260)=4.32$, $p<.001$, $\eta^2_{\text{partial}}=.144$, were statistically significant. Thus, we repeated the ANOVA including only the within-subjects factor of condition (rest, non-affective, affective touch) at each scalp site. The main effect of condition was statistically significant for prefrontal, $F(2,52)=5.88$, $p=.009$, $\eta^2_{\text{partial}}=.18$, frontal, $F(2,52)=4.91$, $p=.018$, $\eta^2_{\text{partial}}=.16$, central, $F(2,52)=5.67$, $p=.005$, $\eta^2_{\text{partial}}=.18$, parietal, $F(2,52)=4.17$, $p=.021$, $\eta^2_{\text{partial}}=.14$, and temporal

$F(2,52)=4.$, $p=.023$, $\eta^2_{\text{partial}}=.14$, but not occipital, $F(2,52)=.06$, $p=.938$, $\eta^2_{\text{partial}}=.01$, scalp sites. Post-hoc pairwise comparisons with Bonferroni correction indicated no difference in alpha activity between affective and non-affective touch across any scalp site, $p's > .05$; however, statistically significant lower alpha activity was found in the non-affective touch, as compared to rest conditions, across prefrontal, frontal, central, parietal, and temporal scalp sites – as well as lower alpha activity in the affective touch as compared to rest conditions in prefrontal and central scalp sites (see Table 3). Moreover, when averaging across touch conditions, we found lower alpha activity in the touch conditions relative to rest in prefrontal, $t(26)=3.04$, $p=.005$, frontal, $t(26)=2.88$, $p=.008$, central, $t(26)=3.05$, $p=.005$, parietal, $t(26)=2.21$, $p=.036$, and temporal, $t(26)=2.66$, $p=.013$, scalp sites. Taken together, these analyses suggest a more general difference in alpha activity between touch and rest conditions, rather than specific effects associated with affective touch (see also descriptives presented in Table 1).

[Table 3]

Beta

Analyses on beta activity showed that the main effects of condition, $F(2,52)=11.65$, $p<.001$, $\eta^2_{\text{partial}}=.31$, scalp site, $F(5,130)=13.14$, $p<.001$, $\eta^2_{\text{partial}}=.336$, and their interaction, $F(10,260)=3.241$, $p=.021$, $\eta^2_{\text{partial}}=.10$, were statistically significant. Therefore, we repeated the ANOVA including only the within-subjects factor of condition (rest, non-affective, affective touch) at each scalp site. The main effect of condition was statistically significant for frontal, $F(2,52)=14.6$, $p<.001$, $\eta^2_{\text{partial}}=.36$, central, $F(2,52)=12.43$, $p<.001$, $\eta^2_{\text{partial}}=.32$, parietal, $F(2,52)=11.13$, $p<.001$, $\eta^2_{\text{partial}}=.30$, and temporal, $F(2,52)=3.58$, $p=.035$, $\eta^2_{\text{partial}}=.12$, scalp sites, but no difference between conditions was reported for prefrontal, $F(2,52)=2.04$, $p=.157$,

$\eta^2_{\text{partial}}=.07$ and occipital, $F(2,52)=1.162$, $p=.321$, $\eta^2_{\text{partial}}=.04$, scalp sites. Except for parietal scalp sites, post-hoc pairwise comparisons with Bonferroni correction indicate no difference in beta activity between affective and non-affective touch across any scalp site, $p>.05$; however, we found lower beta activity in both touch conditions (affective and non-affective touch) relative to rest conditions in frontal and central scalp sites (see Table 4; although significant lower beta activity was only found in the affective touch versus rest conditions, and not in the non-affective touch versus rest conditions, in temporal regions). Taken together, and similar to alpha, these analyses suggest a more general difference in beta activity between touch and rest conditions in frontal and central scalp sites (see also descriptives presented in Table 1). However, we did find a similar pattern of beta activity, as observed in theta activity, in response to affective touch versus non-affective touch and rest, but this was limited to the parietal scalp site.

[Table 4]

Gamma

Analyses on gamma activity showed that while there was a main effect of scalp site, $F(5,130)=14.77$, $p<.001$, $\eta^2_{\text{partial}}=.36$, there was no main effect of condition, $F(2,52)=.69$, $p=.467$, $\eta^2_{\text{partial}}=.03$, and condition did not interact with scalp site, $F(10,260)=.46$, $p=.765$, $\eta^2_{\text{partial}}=.02$. Taken together, these analyses suggest that the effects of affective vs. non-affective touch do not differentiate gamma when recorded at rest.

In sum, theta activity was decreased in response to affective touch, as compared to non-affective touch and rest conditions across multiple scalp sites. However, differential modulation of neural oscillations as a function of affective versus non-affective tactile stimulation was not

observed in any other frequency band, with the exception noted that beta activity was decreased in response to affective touch, as compared to non-affective touch and rest conditions, in parietal scalp sites. Modulation of alpha and beta were also noted primarily at frontal and central scalp sites as a function of tactile (affective and non-affective touch) versus non-tactile conditions, suggesting both types of touch modulated alpha and beta rather than indicating specific effects associated with affective touch.

Discussion

Convergent research suggests that tactile interactions are of developmental importance to social and emotional interactions across species. To understand the affective component of tactile stimulation, neuroimaging studies have begun to elucidate the neural mechanisms that underpin the rewarding and beneficial effects of slow, gentle touch. The current study sought to extend this emerging body of work, examining whether affective touch modulated EEG oscillations.

Consistent with our hypothesis we found suppression of alpha and beta activity as a function of tactile versus non-tactile/rest conditions across multiple scalp sites. Further, while theta activity was not differentiated between the non-affective touch and rest conditions, affective touch, relative to these latter experimental conditions, was associated with decreased theta activity measured across multiple scalp regions. Importantly, this differential modulation of theta as a function of affective versus non-affective tactile stimulation was not observed in any other frequency band – with the exception of beta activity in parietal scalp sites. Together, these findings suggest theta oscillations in particular may be a potential neural signature of slow, affective touch. These findings, and consideration of their limitations and directions for future research, will be discussed in more detail below.

Alpha and Beta

Our finding that touch, irrespective of its affective valence, decreased alpha and beta activity, mostly at frontal and central scalp sites, is consistent with prior literature on tactile stimulation (Diego et al., 2004; Michail et al., 2016; Singh et al., 2014). Alpha and beta oscillations are thought to play a critical role in the somatosensory system for the processing of tactile stimuli (Bauer, Oostenveld, Peeters, & Fries, 2006; Michail et al., 2016; Singh et al., 2014), with beta oscillations in particular being involved in binding processes within somatosensory cortical areas (Brovelli et al., 2004; Simoes, Jensen, Parkkonen, & Hari, 2002). However, as with previous literature (e.g., Michail et al., 2016) but also specific to our design, we cannot overlook that alpha and beta modulation observed here is associated with differences in attention/alertness rather than for the tactile domain per se. In particular, increased alpha activity has been observed in anticipatory periods preceding a sensory stimulus (Foxe et al., 1998), and in anxious participants, increased alpha has been associated with preparedness to process incoming sensory information (Knyazev, Savostyanov, & Levin, 2006). Consequently, it is possible that the differences in alpha and beta activity observed here between the touch and rest conditions, namely increased alpha/beta activity in rest as compared to the touch conditions, could be due to anticipatory effects preceding the touch trials. Critically, although these findings on beta and alpha point to general effects of touch versus rest, we also found that affective touch modulated beta activity, although only at parietal scalp sites. Modulation of beta activity at parietal scalp sites has been previously observed to differentiate between pleasant and unpleasant tactile sensations by fabrics, suggesting that these signals may be related to the affective representation of tactile stimuli (Singh et al., 2014). Interestingly, this modulation of beta

oscillations at parietal scalp sites in response to slow, affective touch resembles our findings with theta activity.

Theta

In contrast to previous research indicating enhanced theta activity in response to A β -mediated discriminative touch (Michail et al., 2016), non-affective touch versus non-tactile/rest conditions did not yield any differences in theta activity across any scalp site. Such findings are in opposition to a growing body of research suggesting that higher amplitude in theta oscillations may reflect involuntary attention drawn from salient sensory stimuli (Iannetti et al., 2008; Wang, Mouraux, Liang & Iannetti, 2010). Yet, it is possible that non-affective touch in this context may not have been perceived as salient, given that the tactile stimuli was delivered in an ‘expected’ manner (e.g., each trial had the same velocity, time, and always followed rest), and was a relatively low pressure tactile stimulation (c.f., Michail et al., 2016).

Central to the current study was our findings that affective touch decreased theta activity, relative to the non-affective touch and rest condition. The attenuation of theta was observed at multiple sites recorded across the scalp. This finding was counter to our hypotheses given preliminary research that reported enhanced theta in response to pleasant forms of skin-to-skin contact in an infant (Maulsby, 1971), as well as theta synchronization that matched the time-course of an ultra-late potential correlating with CT input (Ackerley et al., 2013). Furthermore, prior research has also documented that slow CT stimulation carries positive affective valence (Loken, Wessberg, McGlone, & Olausson, 2009; Pawling et al., 2017) and enhanced theta power has reliably been observed during the processing of affectively-valenced cues (Aftanas et al., 2001, 2002, 2004; Balconi & Pozzoli, 2009; Krause et al., 2000). In an unrelated literature, enhanced theta has also been shown in relaxation processes (including meditation, Aftanas &

Golocheikine, 2001; Stancak et al., 1991; and massage, Diego et al., 2004; Field et al., 1996).

Thus, what might underscore this theta suppression in response to affective touch?

Theta oscillations may occur in states of alertness, fixed concentration, as well as in states of drowsiness (see Mitchell et al., 2008 for a review). This paradoxical presence of theta across seemingly contrasting conditions is thought to be driven either by an inhibitory mechanism that blocks incoming information when focusing attention or going to sleep; or alternatively, by distinct underlying mechanisms that present comparable theta oscillations at the surface of the scalp (Mitchell et al., 2008). Intriguingly, only a handful of studies have reported an attenuation of theta activity. For example, Tanaka et al. (2014) found during rest periods that long-term, relative to short-term, mindfulness practitioners had lower levels of theta activity. This attenuated theta activity in mindfulness experts may reflect the expert practitioner's ability to limit the processing of unnecessary information to facilitate awareness and acceptance of the context in which they exist, akin to a bottom-up regulatory process (Chiesa, Serreti, & Jacobsen, 2013). Similarly, attenuated theta has been found in meditation practices involving emotional regulation (Yu et al., 2011), with an independent study demonstrating that distraction as an emotion regulation strategy also decreased theta activity (Uusberg, Thiruchselvam, & Gross, 2014). Consequently, one interpretation of our finding that affective touch decreased theta may reflect similar attentional-emotional regulatory processes that have been observed in this prior mindfulness, meditation, and emotion regulatory research – and would be consistent with a broader literature on gentle touch at CT-optimal speeds, relative to non-CT optimal speeds, influencing affective regulatory functioning (Fairhurst, Loken, & Grossman, 2014; Liljencontrantz et al., 2016; Morrison, 2016; Pawling et al., 2017). Nevertheless, future research is required to substantiate this interpretation.

Delta and Gamma

Our findings suggest that delta and gamma were not modulated by affective, or non-affective touch, versus rest conditions. Although some studies have found increased delta and gamma activity in response to touch (e.g., Diego et al., 2004; Michail et al., 2016, respectively), many others have not (e.g., Ackerley et al., 2013; Singh et al., 2014). Moreover, these frequencies, and particularly gamma, have been found to be similarly modulated by different sensory modalities (e.g., pain and touch; Mouraux & Iannetti, 2009), highlighting their role in sensory saliency rather than modality-specific processing (Knyazev, 2007; Legrain et al., 2009). Interestingly though, Diego and colleagues (2004) found enhanced delta activity during massage, accompanied by a decrease in heart rate activity, consistent with the notion that delta power is also associated with decreased arousal and relaxation (Niedermeyer, 1982).

Limitations and Future Directions

In summary, our main finding suggests that theta oscillations encode for affective touch: decreased theta activity in response to affective touch versus non-affective touch and rest conditions. Although we report a general response in alpha and beta ranges to tactile stimulation, these frequencies do not seem to code specifically for affective touch, but rather an off/on like response characteristic to tactile stimuli in general. However, we also found modulation of beta activity in parietal scalp sites in response to affective touch, consistent with prior research suggesting that these signals may reflect the affective representation of tactile stimuli (Singh et al., 2014). Our findings should be considered in light of study limitations and directions for future research. First, given that our paradigm required participants to remain in a still position with their eyes closed, our procedure may have led to a low arousal state and drowsiness, which in turn could have influenced EEG dynamics, and particularly theta activity (Klimesch et al.,

1999; Mitchell et al., 2008; Knyazev, Savostyanov, & Levin, 2006). Future research, including physiological measures, is necessary to examine this EEG modulation in response to slow touch, varying the context in which EEG is recorded.

Second, our findings do not speak to whether affective touch modulation of theta and parietal-beta were mediated by bottom-up physiological mechanisms linked to CT stimulation in response to slow tactile stimulation, top-down learned expectations of pleasantness linked to slow tactile stimulation, or both (Ellingsen et al., 2015; von Mohr & Fotopoulou, in press). Indeed, several studies have shown that touch at slow, CT-optimal speeds (versus fast, non-CT optimal speeds) leads to increased self-reported feelings of pleasantness in both CT skin and non-CT skin (e.g., Ackerley, Carlsson, Wester, Olausson, & Backlund Wasling, 2014; Pawling et al., 2017), with such effects in non-CT skin possibly due to secondary reinforcement (McGlone et al., 2014). Consequently, both forms of stimulation may be experienced as pleasant at a subjective level. Nevertheless, tactile stimulation at slow CT-optimal speeds has been shown to give rise to higher BOLD responses in posterior insula than faster non-CT optimal speeds – suggesting specificity in the neural consequences of tactile stimuli of varying speeds and their corresponding frequencies (Morrison et al., 2011). Thus, although we speculate a similar phenomenon in the current study, future investigations examining the effects of CT-optimal touch on theta and parietal-beta in CT versus non-CT skin are needed to provide insight into potential neural coupling between these frequencies and their specific role in encoding slow tactile stimulation.

Relatedly, it is important to note that the frequency of tactile stimulation itself may have influenced theta and parietal-beta oscillations, independent of the pleasantness/valence of the stimulus. To address this important point, future work should move beyond the forearm to

examine other areas of skin that may have variation in CT innervation. The inclusion of such similar tactile stimulation in other body parts, where CT afferents are not thought to innervate, could also control for potential confounders, including the frequency of tactile stimulation associated with slow, affective versus fast, non-affective touch. Such work should incorporate subjective (self-reported mood, perceived pleasantness) measures to directly examine the relationship between the subjective experience of pleasantness and modulation of theta and parietal-beta neural oscillations. Alternatively, given studies suggesting similar effects of pleasantness in response to relatively slow touch in both CT-skin and non-CT skin (e.g., Ackerley et al., 2014; Pawling et al., 2017), another approach could include other frequencies of stimulation (within the CT-optimal range, e.g., 3 cm/s and 6 cm/s and outside the CT-optimal range, e.g., 0.3 cm/s and 30 cm/s) in CT-skin that are thought to give rise to similar feelings of pleasantness while allowing control over the frequency of tactile stimulation.

Third, our sample were young adults. It would be valuable to examine the modulation of affective touch across development to determine whether attenuated theta activity occurs across the lifespan. Given that the EEG technique confers the advantage of providing a complete lifespan perspective assessment of neural correlates, this line of work could extend prior knowledge on the maturation of brain mechanisms for processing affective touch throughout development (Bjornsdotter, Gordon, Pelphrey, Olausson, & Kaiser, 2014).

Fourth, future research should examine dispositional and contextual factors that bear on touch and neuromodulation. For instance, under a given context, an individual might experience affective touch as arousing, rather than soothing (Ellingsen et al., 2015). Since the experimenters administering touch in the present study were female, it is possible that gender effects associated with arousal in response to the touch might have played a role in variations of theta activity

across our sample. We were underpowered to discern sex differences in neural response to touch in the current sample but plan to explore sex effects in future research. Relatedly, individual differences in how we seek and respond to touch may also influence the regulatory functions of this sensory-affective modality (Voos et al., 2013).

Finally, further investigations are necessary to elucidate whether affective touch impacts other aspects of functioning, including the functional significance of CT-mediated sympathetic skin response (Olausson et al., 2008) and its relationship with arousal, sympathetic/parasympathetic activity, and EEG oscillations. This work would be facilitated by collecting objective (skin conductance, heart rate variability) measurements from participants before, during, and after exposure to affective and non-affective touch.

In conclusion, tactile interactions play a central role in social and emotional interactions across development. Understanding the neural correlates of affective touch provides an important insight into the mechanisms that underscore this critical sensory modality that is often overlooked in social neuroscience research. Here we report a response in alpha and beta activity to touch in general, and theta activity in particular to affective touch. Similar to theta, we find a similar pattern of activity in response to affective touch in beta oscillations, although only in parietal scalp sites. The pattern of these findings suggests that alpha/beta ranges may follow an off/on like characteristic to tactile stimuli in general, whereas theta and parietal-beta ranges may reflect attentional-emotional regulatory mechanisms linked to stroking at the velocity of affective touch and the affective representation of tactile stimuli, respectively. Future work is needed to provide insight into potential neural coupling between these two latter frequencies and their specific role in encoding slow tactile stimulation.

References

- Ackerley, R., Carlsson, I., Wester, H., Olausson, H., & Wasling, H. B. (2014). Touch perceptions across skin sites: differences between sensitivity, direction discrimination and pleasantness. *Frontiers in Behavioral Neuroscience*, 8.
- Ackerley, R., Eriksson, E., & Wessberg, J. (2013). Ultra-late EEG potential evoked by preferential activation of unmyelinated tactile afferents in human hairy skin. *Neuroscience letters*, 535, 62-66.
- Aftanas, L. I., & Golocheikine, S. A. (2001). Human anterior and frontal midline theta and lower alpha reflect emotionally positive state and internalized attention: high-resolution EEG investigation of meditation. *Neuroscience letters*, 310(1), 57-60.
- Aftanas, L. I., Reva, N. V., Varlamov, A. A., Pavlov, S. V., & Makhnev, V. P. (2004). Analysis of evoked EEG synchronization and desynchronization in conditions of emotional activation in humans: temporal and topographic characteristics. *Neuroscience and behavioral physiology*, 34(8), 859-867.
- Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2001). Affective picture processing: event-related synchronization within individually defined human theta band is modulated by valence dimension. *Neuroscience letters*, 303(2), 115-118.
- Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2002). Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *International Journal of Psychophysiology*, 44(1), 67-82.
- Agren, G., Lundeberg, T., Uvnäs-Moberg, K., & Sato, A. (1995). The oxytocin antagonist 1-deamino-2-D-Tyr-(Oet)-4-Thr-8-Orn-oxytocin reverses the increase in the withdrawal

- response latency to thermal, but not mechanical nociceptive stimuli following oxytocin administration or massage-like stroking in rats. *Neuroscience letters*, 187(1), 49-52.
- Balconi, M., & Pozzoli, U. (2009). Arousal effect on emotional face comprehension: frequency band changes in different time intervals. *Physiology & behavior*, 97(3), 455-462.
- Bauer, M., Oostenveld, R., Peeters, M., & Fries, P. (2006). Tactile spatial attention enhances gamma-band activity in somatosensory cortex and reduces low-frequency activity in parieto-occipital areas. *Journal of Neuroscience*, 26(2), 490-501.
- Bennett, R. H., Bolling, D. Z., Anderson, L. C., Pelphrey, K. A., & Kaiser, M. D. (2014). fNIRS detects temporal lobe response to affective touch. *Social cognitive and affective neuroscience*, 9(4), 470-476.
- Björnsdotter, M., Gordon, I., Pelphrey, K. A., Olausson, H., & Kaiser, M. (2014). Development of brain mechanisms for processing affective touch. *Frontiers in behavioral neuroscience*, 8, 24.
- Björnsdotter, M., Morrison, I., & Olausson, H. (2010). Feeling good: on the role of C fiber mediated touch in interoception. *Experimental brain research*, 207(3-4), 149-155.
- Brauer, J., Xiao, Y., Poulain, T., Friederici, A. D., & Schirmer, A. (2016). Frequency of Maternal Touch Predicts Resting Activity and Connectivity of the Developing Social Brain. *Cerebral Cortex*, bhw137.
- Brovelli, A., Ding, M., Ledberg, A., Chen, Y., Nakamura, R., & Bressler, S. L. (2004). Beta oscillations in a large-scale sensorimotor cortical network: directional influences revealed by Granger causality. *Proceedings of the National Academy of Sciences of the United States of America*, 101(26), 9849-9854.

- Cantero, J. L., & Atienza, M. (2005). The role of neural synchronization in the emergence of cognition across the wake-sleep cycle. *Reviews in the Neurosciences*, *16*(1), 69-84.
- Chiesa, A., Serretti, A., & Jakobsen, J. C. (2013). Mindfulness: Top-down or bottom-up emotion regulation strategy?. *Clinical psychology review*, *33*(1), 82-96.
- Diego, M. A., Field, T., Sanders, C., & Hernandez-Reif, M. (2004). Massage therapy of moderate and light pressure and vibrator effects on EEG and heart rate. *International Journal of Neuroscience*, *114*(1), 31-44.
- Ellingsen, D. M., Leknes, S., Løseth, G., Wessberg, J., & Olausson, H. (2015). The neurobiology shaping affective touch: expectation, motivation, and meaning in the multisensory context. *Frontiers in psychology*, *6*.
- Field, T. (2010). Touch for socioemotional and physical well-being: A review. *Developmental Review*, *30*(4), 367-383.
- Field, T. (2014). Massage therapy research review. *Complementary therapies in clinical practice*, *20*(4), 224-229.
- Field, T., Ironson, G., Scafidi, F., Nawrocki, T., Goncalves, A., Burman, I., ... & Kuhn, C. (1996). Massage therapy reduces anxiety and enhances EEG pattern of alertness and math computations. *International Journal of Neuroscience*, *86*(3-4), 197-205.
- Foxe, J.J., Simpson, G.V., & Ahlfors, S.P. (1998). Parieto-occipital approximately 10Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport* *9*, 3929-3933.
- Gordon, I., Voos, A. C., Bennett, R. H., Bolling, D. Z., Pelphrey, K. A., & Kaiser, M. D. (2011). Brain mechanisms for processing affective touch. *Human Brain Mapping*, *34*(4), 914-922.

- Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and clinical neurophysiology*, 55(4), 468-484. doi: 10.1016/0013-4694(83)90135-9
- Hathaway, E. E., Luberto, C. M., Bogenschutz, L. H., Geiss, S., Wasson, R. S., & Cotton, S. (2015). Integrative care therapies and physiological and pain-related outcomes in hospitalized infants. *Global Advances in Health and Medicine*, 4(4), 32-37.
- Hertenstein, M. J., Keltner, D., App, B., Buleit, B. A., & Jaskolka, A. R. (2006). Touch communicates distinct emotions. *Emotion*, 6(3), 528.
- Iannetti, G. D., Hughes, N. P., Lee, M. C., & Mouraux, A. (2008). Determinants of laser-evoked EEG responses: pain perception or stimulus saliency?. *Journal of neurophysiology*, 100(2), 815-828.
- Jacobs, G. D., & Lubar, J. F. (1989). Spectral analysis of the central nervous system effects of the relaxation response elicited by autogenic training. *Behavioral Medicine*, 15(3), 125-132.
- Johansson, R. S., & Vallbo, Å. B. (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *The Journal of physiology*, 286(1), 283-300.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain research reviews*, 29(2), 169-195.
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in cognitive sciences*, 16(12), 606-617.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain research reviews*, 53(1), 63-88.

- Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience & Biobehavioral Reviews*, *31*(3), 377-395.
- Knyazev, G. G., Savostyanov, A. N., & Levin, E. A. (2006). Alpha synchronization and anxiety: implications for inhibition vs. alertness hypotheses. *International Journal of Psychophysiology*, *59*(2), 151-158.
- Korosi, A., & Baram, T. Z. (2010). Plasticity of the stress response early in life: mechanisms and significance. *Developmental psychobiology*, *52*(7), 661-670.
- Krahé, C., Drabek, M., Paloyelis, Y., & Fotopoulou, A. (2016). Affective touch and attachment style modulate pain: a laser-evoked potentials study. *Philosophical Transactions of the Royal Society B*, *371*(1708), 20160009.
- Krause, C. M., Viemerö, V., Rosenqvist, A., Sillanmäki, L., & Åström, T. (2000). Relative electroencephalographic desynchronization and synchronization in humans to emotional film content: an analysis of the 4–6, 6–8, 8–10 and 10–12 Hz frequency bands. *Neuroscience letters*, *286*(1), 9-12.
- Liljencrantz, J., Strigo, I., Ellingsen, D. M., Krämer, H. H., Lundblad, L. C., Nagi, S. S., ... & Olausson, H. (2017). Slow brushing reduces heat pain in humans. *European Journal of Pain*, *21*(7), 1173-1185.
- Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*(6843), 150-157.
- Löken, L. S., Wessberg, J., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature neuroscience*, *12*(5), 547-548.

- Maulsby, R. L. (1971). An illustration of emotionally evoked theta rhythm in infancy: Hedonic hypersynchrony. *Electroencephalography and Clinical Neurophysiology*, 31(2), 157-165.
- McGlone, F., Wessberg, J., & Olausson, H. (2014). Discriminative and affective touch: sensing and feeling. *Neuron*, 82(4), 737-755.
- Michail, G., Dresel, C., Witkovský, V., Stankewitz, A., & Schulz, E. (2016). Neuronal oscillations in various frequency bands differ between pain and touch. *Frontiers in human neuroscience*, 10.
- Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal “theta”. *Progress in neurobiology*, 86(3), 156-185.
- Morrison, I. (2016). Keep calm and cuddle on: social touch as a stress buffer. *Adaptive Human Behavior and Physiology*, 1-19.
- Morrison, I., Björnsdotter, M., & Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. *The Journal of Neuroscience*, 31(26), 9554-9562.
- Mouraux, A., & Iannetti, G. D. (2009). Nociceptive laser-evoked brain potentials do not reflect nociceptive-specific neural activity. *Journal of neurophysiology*, 101(6), 3258-3269.
- Nelson, E. E., & Panksepp, J. (1998). Brain substrates of infant–mother attachment: contributions of opioids, oxytocin, and norepinephrine. *Neuroscience & Biobehavioral Reviews*, 22(3), 437-452.
- Nunez, P. L. (2000). Toward a quantitative description of large-scale neocortical dynamic function and EEG. *Behavioral and Brain Sciences*, 23(03), 371-398.
- Olausson, H., Cole, J., Rylander, K., McGlone, F., Lamarre, Y., Wallin, B. G., ... & Vallbo, Å. (2008). Functional role of unmyelinated tactile afferents in human hairy skin:

- sympathetic response and perceptual localization. *Experimental Brain Research*, 184(1), 135-140.
- Pawling, R., Cannon, P. R., McGlone, F. P., & Walker, S. C. (2017). C-tactile afferent stimulating touch carries a positive affective value. *PloS one*, 12(3), e0173457.
- Perini, I., & Olausson, H., & Morrison, I. (2015). Seeking pleasant touch: neural correlates of behavioral preferences for skin stroking. *Frontiers in behavioral neuroscience*, 9, 8.
- Simões, C., Jensen, O., Parkkonen, L., & Hari, R. (2003). Phase locking between human primary and secondary somatosensory cortices. *Proceedings of the National Academy of Sciences*, 100(5), 2691-2694.
- Singh, H., Bauer, M., Chowanski, W., Sui, Y., Atkinson, D., Baurley, S., ... & Bianchi-Berthouze, N. (2014). The brain's response to pleasant touch: an EEG investigation of tactile caressing. *Frontiers in human neuroscience*, 8.
- Stancak Jr, A., Kuna, M., Dostalek, C., & Vishnudevananda, S. (1990). Kapalabhati--yogic cleansing exercise. II. EEG topography analysis. *Homeostasis in health and disease: international journal devoted to integrative brain functions and homeostatic systems*, 33(4), 182-189.
- Suvilehto, J. T., Glerean, E., Dunbar, R. I., Hari, R., & Nummenmaa, L. (2015). Topography of social touching depends on emotional bonds between humans. *Proceedings of the National Academy of Sciences*, 112(45), 13811-13816.
- Tanaka, G. K., Peressutti, C., Teixeira, S., Cagy, M., Piedade, R., Nardi, A. E., ... & Velasques, B. (2014). Lower trait frontal theta activity in mindfulness meditators. *Arquivos de neuro-psiquiatria*, 72(9), 687-693.

- Trotter, P. D., McGlone, F., McKie, S., McFarquhar, M., Elliott, R., Walker, S. C., & Deakin, J. F. W. (2016). Effects of acute tryptophan depletion on central processing of CT-targeted and discriminatory touch in humans. *European Journal of Neuroscience*, 44(4), 2072-2083.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalography and clinical neurophysiology*, 87(3), 154-163.
- Uusberg, A., Thiruchselvam, R., & Gross, J. J. (2014). Using distraction to regulate emotion: Insights from EEG theta dynamics. *International Journal of Psychophysiology*, 91(3), 254-260.
- Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nature reviews neuroscience*, 2(4), 229-239.
- von Mohr, M., & Fotopoulou, A. (in press). The cutaneous borders of interoception: Active inference of pain and pleasure on the skin.
- Voos, A. C., Pelphey, K. A., & Kaiser, M. D. (2013). Autistic traits are associated with diminished neural response to affective touch. *Social cognitive and affective neuroscience*, 8(4), 378-386.
- Wang, A. L., Mouraux, A., Liang, M., & Iannetti, G. D. (2010). Stimulus novelty, and not neural refractoriness, explains the repetition suppression of laser-evoked potentials. *Journal of neurophysiology*, 104(4), 2116-2124.
- Yu, X., Fumoto, M., Nakatani, Y., Sekiyama, T., Kikuchi, H., Seki, Y., ... & Arita, H. (2011). Activation of the anterior prefrontal cortex and serotonergic system is associated with improvements in mood and EEG changes induced by Zen meditation practice in novices. *International Journal of Psychophysiology*, 80(2), 103-111.

Author Notes

Acknowledgments

This work was supported by the Anna Freud Centre (UK) and the National Council on Science and Technology (CONACyT- 538843; Mexico) scholarship (to M.V.M.).

Declaration of Conflicting Interests

The authors report no conflicts of interest related to their authorship or the publication of this article.

Table 1.

Log-transformed spectral power for delta, theta, alpha, beta and gamma recorded from the rest, non-affective touch, and affective touch conditions in prefrontal, frontal, central, temporal, parietal and occipital regions. Data is presented as mean (standard deviation).

	Prefrontal	Frontal	Central	Parietal	Temporal	Occipital
Delta						
Affective touch	2.17(.69)	1.51(.56)	1.00(.44)	1.08(.66)	1.06(.79)	1.09(.57)
Non-affective touch	2.19(.66)	1.49(.59)	1.05(.48)	1.03(.65)	.99(.87)	1.06(.64)
Rest	2.19(.67)	1.50(.59)	1.09(.58)	1.02(.65)	1.09(.78)	1.04(.56)
Theta						
Affective touch	-.49(.49)	-.85(.50)	-.84(.50)	-.87(.54)	-1.02(.67)	-.63(.66)
Non-affective touch	-.39(.55)	-.73(.49)	-.63(.59)	-.44(.77)	-.91(.67)	-.57(.67)
Rest	-.42(.53)	-.78(.46)	-.73(.55)	-.75(.46)	-.93(.56)	-.59(.65)
Alpha						
Affective touch	-.25(.79)	-.30(.86)	-.24(.91)	.19(.95)	-.13(1.0)	.81(1.12)
Non-affective touch	-.23(.85)	-.30(.89)	-.20(.91)	.26(.94)	-.13(.97)	.81(1.12)
Rest	-.16(.83)	-.23(.86)	-.13(.93)	.29(.98)	-.07(.98)	.81(1.11)
Beta						
Affective touch	-2.05(.64)	-2.47(.46)	-2.49(.48)	-2.34(.47)	-2.29(.60)	-1.74(.62)
Non-affective touch	-2.05(.61)	-2.45(.46)	-2.45(.48)	-2.27(.45)	-2.26(.64)	-1.72(.64)
Rest	-2.01(.59)	-2.38(.42)	-2.38(.49)	-2.24(.46)	-2.23(.59)	-1.71(.59)
Gamma						
Affective touch	-3.03(1.01)	-3.41(1.04)	-2.62(1.49)	-1.44(1.96)	-3.22(.95)	-2.88(1.17)
Non-affective touch	-3.03(1.00)	-3.40(1.06)	-2.58(1.53)	-1.43(1.97)	-3.20(.98)	-2.86(1.18)
Rest	-3.04(.99)	-3.40(1.06)	-2.60(1.51)	-1.46(1.95)	-3.21(.99)	-2.89(1.14)

Note. Greater negative values in log-transformed data reflect lower activity.

Table 2.

Post-hoc pairwise comparisons with Bonferroni correction on log-transformed theta activity between conditions (affective touch, non-affective touch, and rest) across scalp sites (prefrontal, frontal, central, parietal, temporal and occipital). Data is presented as mean difference (standard error). Asterisks indicate * $p < .05$, ** $p < .01$ corrected values. Plus sign indicates a trend towards statistical significance (i.e., + $p = .059$, + $p = .052$, + $p = .059$).

	Prefrontal	Frontal	Central	Parietal	Temporal	Occipital
Affective vs. non-affective touch	.10(.03)*	.13(.04)*	.22(.08)+	.42(.12)**	.11(.04)*	.14(.05)*
Affective touch vs. rest	.07(.03)+	.07(.03)*	.12(.03)**	.11(.04)*	.09(.03)**	.04(.03)
Non-affective touch vs. rest	.02(.02)	.05(.04)	.10(.03)	.31(.16)+	.02(.03)	.10(.05)

Table 3.

Post-hoc pairwise comparisons with Bonferroni correction on log-transformed alpha activity between conditions (affective touch, non-affective touch, and rest) across scalp sites (prefrontal, frontal, central, parietal, and temporal). Data is presented as mean difference (standard error). Asterisks indicate * $p < .05$, ** $p < .01$ corrected values.

	Prefrontal	Frontal	Central	Parietal	Temporal
Affective vs. non-affective touch	.01(.02)	.01(.02)	.04(.03)	.07(.04)	.01(.02)
Affective touch vs. rest	.09(.03)*	.07(.03)	.11(.04)*	.03(.03)	.07(.03)
Non-affective touch vs. rest	.08(.03)*	.07(.02)**	.08(.04)*	.10(.04)*	.06(.02)*

Table 4.

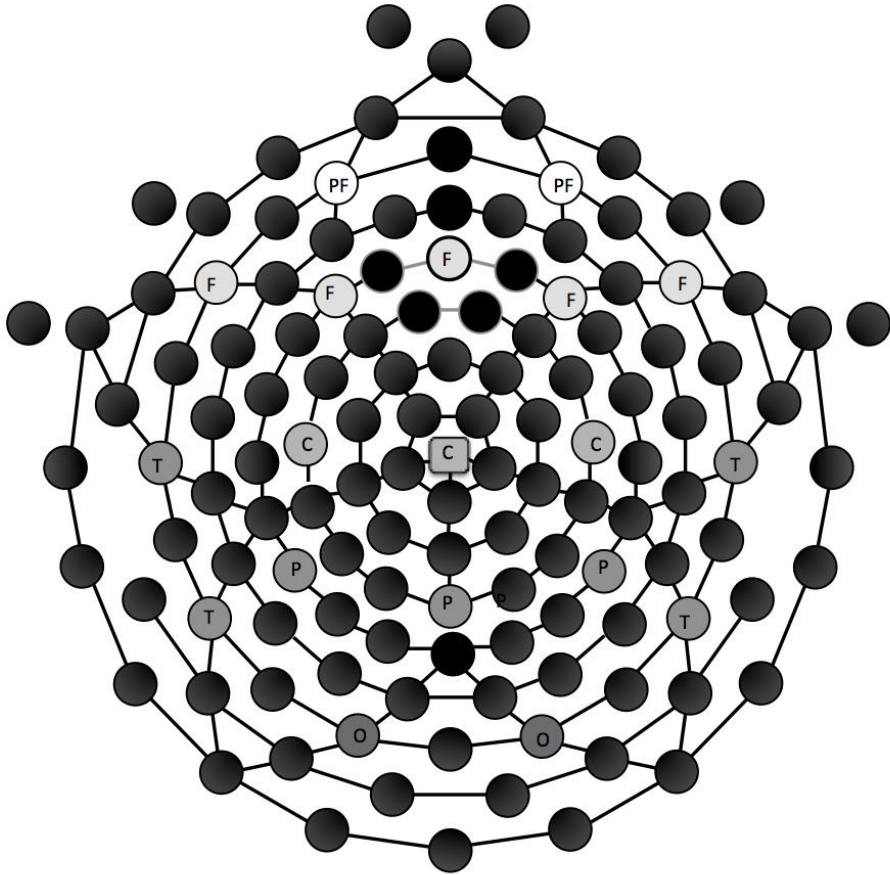
Post-hoc pairwise comparisons with Bonferroni correction on log-transformed beta activity between conditions (affective touch, non-affective touch, and rest) across scalp sites (frontal, central, parietal, and temporal). Data is presented as mean difference (standard error). Asterisks indicate * $p < .05$, ** $p < .01$ corrected values.

	Frontal	Central	Parietal	Temporal
Affective vs. non-affective touch	.02(.02)	.04(.03)	.07(.02)*	.03(.03)
Affective touch vs. rest	.09(.02)**	.11(.02)**	.10(.02)**	.06(.02)*
Non-affective touch vs. rest	.07(.02)**	.07(.02)**	.05(.02)	.03(.02)

Figure Captions

Figure 1. Sensor layout for the 128 lead Geodesic sensor net (Electrical Geodesics, Inc.; Tucker, 1993). Electrodes used in the analysis of the prefrontal (FP1, FP2), frontal (FZ, F3, F4, F7, F8), central (C3, CZ, C4), parietal (P3, PZ, P4), temporal (T3, T4, T5, T6), and occipital (O1, O2) scalp sites are highlighted in white, high light grey, light grey, grey, high dark grey, and dark grey, respectively.

Figure 1



Supplementary Material

Delta Analyses Including the Two Rest Conditions

Given that we found a non-tactile condition by scalp site interaction when analyzing delta activity, $F(5,130)=2.74$, $p=.046$, $\eta^2_{\text{partial}}=.10$, we repeated our repeated-measures ANOVA specifying Condition (affective touch, non-affective touch, affective touch rest, non-affective touch rest) and Scalp Site (prefrontal, frontal, central, parietal, temporal, and occipital) on delta activity. Similar to the analyses in the main text, these analyses on delta activity showed a main effect of scalp site, $F(5,130)=19.31$, $p<.001$, $\eta^2_{\text{partial}}=.43$. However, there was no main effect of condition, $F(2,52)=1.93$, $p=.151$, $\eta^2_{\text{partial}}=.07$, and condition did not interact with scalp site, $F(10,260)=1.97$, $p=.966$, $\eta^2_{\text{partial}}=.07$. Together, these analyses suggest that the effects of affective vs. non-affective touch and rest are not observed in delta activity, even when including the two non-tactile/rest conditions in the ANOVA.