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Right between the eyes: Corrugator muscle activity tracks the changing pleasantness of repeated slow stroking touch

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ABSTRACT

Subjective reports and physiological responses provide different appraisals of sensory input. The coherence between subjective and physiological responses to repeated pleasant stimuli remains largely unexplored, and is particularly important in situations where subjective responses are prone to cognitive or contextual bias. Here, we investigate how subjective and physiological responses to repeated gentle touch correspond at two separate sessions and compare these to responses obtained when smelling an odorant. Forty-eight participants underwent 60 trials of skin-to-skin slow stroking touch directed to the forearm. We collected subjective pleasantness reports, recorded facial electromyography (EMG) of the corrugator and zygomaticus muscles and heart-rate variability (HRV). With increasing touch repetitions, mean ratings of pleasantness decreased and corrugator muscle activity increased during session 1, whereas zygomaticus activity remained largely unchanged during both sessions. HRV was significantly higher during the first session, but did not increase from baseline during either sessions. Touch was rated as more pleasant than odor, and demonstrated greater resilience to satiety than the odor responses. Facial EMG recordings of the corrugator muscle appear to be a relevant measure for capturing satiety effects in skin-to-skin touch. Zygomaticus and HRV responses were independent of the subjective appraisal of the gentle touch. Rather than being blueprints of the subjective reports, physiological responses appear to reflect different parts of the subjective experience. As such, an improved understanding of the subjective and physiological responses to pleasant stimuli may improve our understanding of the dynamic interactions that take place in shaping complex emotional phenomena, such as aversion and pleasantness.

1. Introduction

We express our emotions in many different ways: A subdued sigh of delight from sensing the sunrays on our skin, or a loud roar when scoring a goal in the decisive moment of a football match, are both pleasurable expressions, yet their physiological manifestations are vastly different. These multitudes of subjective expressions and physiological manifestations of emotional states offer considerable possibilities for understanding emotional responses [38]. However, subjective explicit reports are constructed appraisals based on multiple processes, such as autonomic responses and memory and thus represent only selected fragments in a series of processes that ultimately shape an experience [11]. Moreover, not all individuals may be capable of or willing to report their emotional state [35]. In contrast, implicit physiological responses are largely unedited by the conscious mind [38]. Thus, a combination of subjective and physiological measures is required to further our understanding of complex emotional phenomena [65].

Physiological responses to sensory stimuli can be measured by changes in electrocardiogram (ECG) and electromyography (EMG) activity. These physiological responses are frequently employed as autonomic indicators of emotional arousal [7]. Heart rate variability (HRV) is derived from an ECG and indicates the variation of heartbeats within a given timeframe [51]. HRV is considered highly related to the activation of the autonomic nervous system (ANS). Broadly speaking, a high HRV is associated with improved resilience to stress and emotion regulation [2,53,22]. In contrast, facial EMG responses are believed to reflect instantaneous responses to emotionally charged stimuli, due to the high temporal resolution of the EMG signal [52]. Commonly, the corrugator muscle is believed to indicate negative affect, by forming a furrow of the brow ("frowning"). The zygomaticus muscle is believed to indicate positive affect ("smiling") [13]. The rapid detection of EMG

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signals allows for analysis of responses that are willingly or unwillingly suppressed by the participants' expressive behavior. For instance, in a study of prejudices, white students verbally reported a preference for working with black students, but displayed greater negative affect (increased corrugator and reduced zygomaticus activity) towards black students than towards white students [59]. The authors argued that the facial EMG activity reflected uncontrolled, automatic responses that were not accessible from self-reports.

Some diversion between subjective and physiological responses can be found for virtually every measure intended to capture implicit responses to emotional stimuli [35]. For example, in a recent study on the effect of music on emotion and HRV, the self-reported emotional response to music and the HRV response were not related to each other [32]. Specifically, while self-selected music led to higher ratings of perceived joy and engagement than classical music, it also led to a lower HRV than classical music [32]. This suggests a complex interactive process between subjective and physiological mechanisms that are not always compatible.

With our background in affective touch, we set out to study the coherence between subjective and physiological responses to skin-to-skin touch. Such touch has the ability to elicit distinct and very powerful subjective emotional responses [19,25], but the latter do not always seem to be reflected in concomitant changes of physiological responses. Pawling, Cannon, McGlone, and Walker [41] reported a distinct zygomaticus EMG response to touch that was not discernible from the subjective reports alone. However, recent findings by Mayo, Linde, Olausson, Heilig, and Morrison [36] and our group [42] differ somewhat to those results as pleasant touch led to a relaxation of the corrugator muscle, but did not affect the zygomaticus activity. Controversial results are also observed for the correspondence between subjective ratings and HRV in response to touch. Participants rated stroking touch applied for approximately 40 min as less pleasant towards the end than at the start of the experiment [44,55], but the HRV was reported to increase during stroking in another similar study [58]. In a clinical study of patients scheduled for aortic surgery, however, the patients who received therapeutic massage reported a greater reduction in anxiety levels than the control group, but the HRV did not differ between the two groups [31].

We aimed to investigate comprehensively the subjective and physiological responses to repeated gentle touch. This served as “Part 1″ of the experiment. To this end, subjective ratings of pleasantness, facial EMG and ECG data were collected in response to the repeated administration of a gentle, stroking touch. To verify these responses, the same participants attended a second session with identical set-up. Moreover, we aimed to compare the touch responses to those elicited by smelling an odorant, previously reported as mildly pleasant [61]. This served as “Part 2″ of the experiment and was included to control for modality specific effects and effects related to the mere passage of time. Our hypotheses may thus be summarized as follows: Firstly, in line with previous studies on longer-lasting repeated touch [44,55,57], we expected that the subjective pleasantness ratings would drop with increasing repetitions. Secondly, we expected the subjective drop in pleasantness ratings to be accompanied by distinct physiological responses: Specifically, we expected a gradual increase in corrugator activity (indicating increased negative affect towards the touch) and a gradual reduction in zygomaticus activity (indicating decreased positive affect towards the pleasant touch). In line with Triscoli et al. [57], we also expected the HRV to increase with repetitions. All these measures were expected to be similar in session 1 and 2.

2. Methods

2.1. Participants

The sample size was estimated using the online program “Power ANalysis for GEneral Anova designs” (PANGEA) [62,63]. Using a fully crossed within-subject design with an estimated medium effect size of 0.45, forty-five participants were deemed necessary for a power of 0.9. In order to account for potential dropouts, forty-eight people were recruited via flyers and information distributed at TU Dresden and the University Hospital website. The participants reported to be healthy men ($N = 25$) and women ($N = 23$) (mean age 27 ± 4 SD, range 21–38), with no subjectively reported sensory impairments of tactile function. Forty-seven participants took part in two sessions. One participant canceled the second session because of illness, therefore the data for this participant was included for session 1 only.

The study was part of a larger project and included a brief investigation of olfactory responses. Olfactory function was tested using the Sniffin' Sticks Test [23]. Impairments of olfactory function in addition to insufficient comprehension of the German language served as exclusion criteria. Three participants were pregnant at the time of testing. Participants were compensated with 20 Euros for taking part in both sessions. The study was approved by the ethics committee of the Medical Faculty of TU Dresden.

2.2. Study design

The experiment consisted of two sessions (Fig 1). In both sessions, each participant received and rated 60 trials of gentle stroking touch to the left forearm. This constituted *“Part 1″* of the experiment. Afterwards, in one of the sessions, each participant received and rated 30 trials of an odorant. This constituted *“Part 2″* of the experiment. Importantly, *“Part 2″* of the experiment was always performed after the completion of one of the touch sessions and was only repeated once for each participant.

Each session lasted approximately 60 min, including the time for preparation. All participants completed a set of questionnaires on personality and social life in-between session 1 and 2 (data reported elsewhere). Questionnaires were filled in at home and online. Between session 1 and session 2, a mean of 10.7 ± 4.4 SD days passed (range 6–20 days).

2.3. Setup

During the experiment, the participants sat comfortably in a chair in front of a computer screen. Three people served as the main data collectors (two women), of which one was always present during the data collection and was in charge of the facial EMG and HRV preparations. There were always two experimenters present, and the participants were unable to see the actual touch or who was providing the stimulation. This was done as previous studies have shown that participants' responses may be facilitated by observing the actual touch itself [54], by interpersonal dynamics [46,15,9,21,57,64], by being observed or not [24] or by the gender of the experimenter [20,43]. The participant's left arm was positioned on a pillow and shielded from the participant's view by a curtain. A distance of 10 cm was marked on the dorsal forearm to indicate the skin area to be touched. Electrodes for the facial EMG and electrocardiogram (ECG) were applied and connected to the receivers. The experimenter checked the impedance of EMG-electrodes and, if necessary, readjusted the electrodes (see Fig 2 for experimental set-up).

The appearance of an “X” on the screen announced a pending stimulus for the participants. Immediately after the touch, the participants were instructed to rate its perceived pleasantness on a visual analogue scale (VAS) by using a mouse. The VAS was anchored by the words “unpleasant” and “pleasant” (coded as −10 and +10). No time constraint was imposed for rating. The next trial started 30 s after the participant's response. Prior to the experiment, participants completed two practice trials to familiarize themselves with the use of the VAS. The VAS and sounds for timing of the touch were presented via E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA).

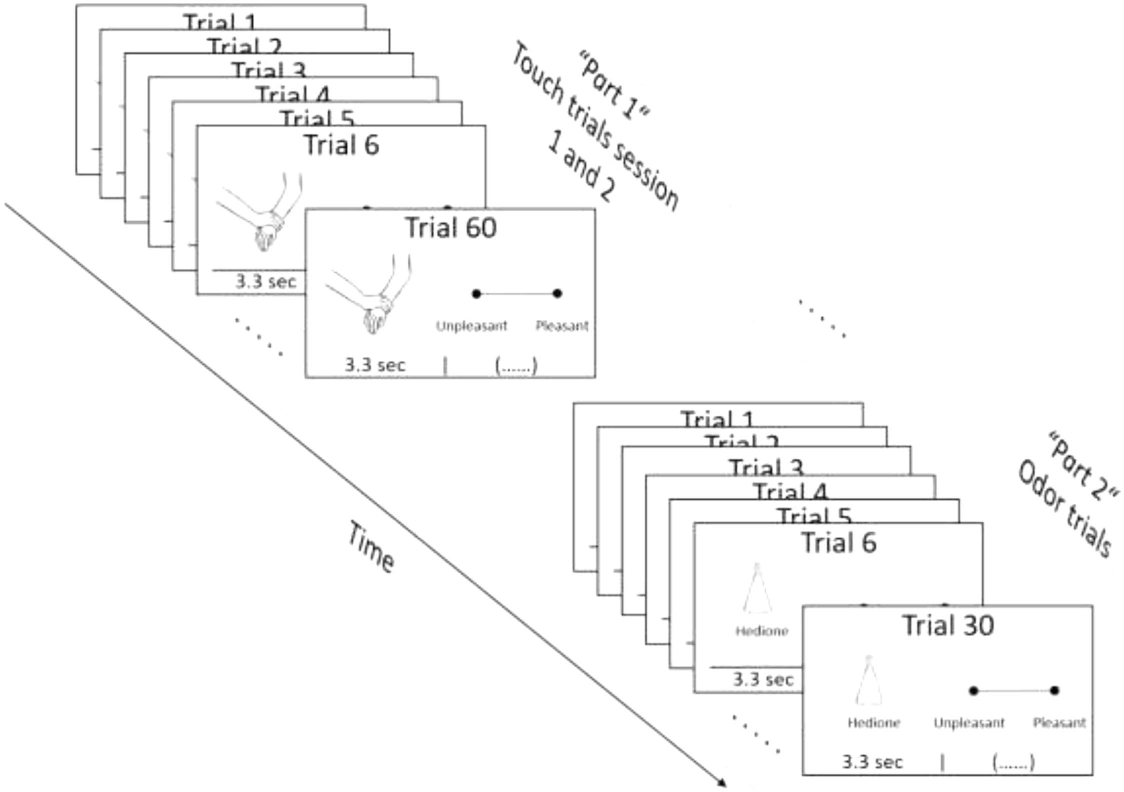

Fig. 1. In part 1 of the study, the participants underwent 60 trials of gentle stroking touch applied to the dorsal forearm in two separate sessions. After each trial, the participants rated the pleasantness of the touch on a visual analogue scale. In part 2 of the study, a subset of 36 participants rated a mildly pleasant odorant following the touch trials in one of the sessions. The odorant was presented 30 times. Facial EMG responses and the electrocardiogram were recorded during both modalities.

Fig. 2. Overview of the experimental set-up.

2.3.1. *Touch stimulation*

The touch was performed manually using the palmar surface of digits 2–4. The experimenter was guided by auditory cues delivered through a pair of headsets to ensure accurate timing and velocity of the strokes. A distance of 10 cm was stroked with a velocity of 3 cm/sec in a proximal-distal direction on the participant's dorsal left forearm. This velocity has been shown to activate a group of afferent tactile fibers, referred to as C-tactile fibers when applied to hairy skin [33] and has been consistently found to be the most pleasant velocity [16,37]. Skin-to-skin stimulation was used because of its greater ecological validity [26] and because healthy participants' responses are similar when touched by hand and brush [49]. The experimenter was trained to perform the touch with constant pressure and velocity using a scale and visual feedback on a screen. Out of consideration for participants with a potential touch aversion, a stop criterion was implemented. Whenever a participant rated five consecutive strokes as "unpleasant" (ratings between −10 to −8), the experiment was prematurely terminated. This criterion was applied to one participant after the 49th touch-trial of session 1.

2.3.2. *Odor stimulation*

The odorant "Hedione" (Firmenich, Meyrin, Switzerland) was presented through a gap in the curtains for 3.3 s. The odorant was contained within an unlabeled opaque glass bottle with a screw lid and an inner diameter of 3 cm. Prior to the inhalation phase of the trial, the lid was removed and the bottle was placed just in front of the participant' lips before the participant was requested to inhale. After approximately 3.3 s, the odorant was removed and the lid was closed.

2.4. *Apparatus*

Facial EMG and ECG data were collected using the BioPac MP150 Nomadix wireless system (BioPac Systems Inc, Santa Barbara, CA, USA). Data was recorded using AcqKnowledge software ([1] version 4.4, BioPac Systems Inc, Ca, USA) and sampled at 1000 kHz.

2.5. *Electromyography*

4 mm Ag/AgCl surface click electrodes with disposable adhesive caps (BioPac Inc, Add204) were filled with electrode gel (BioPac SignaGel 100) and positioned over the *corrugator supercilii* and

zygomaticus major muscles of the left side of the face, as described by Fridlund and Cacioppo [18] and Tassinary et al., [52]. The reference electrode was placed on the participant's forehead. The impedance was checked using the “EL-CHECK” (BioPac Inc, Ca, USA) and was kept below 20 kΩ. The facial EMG data were amplified 5000x, filtered online with 10–500 Hz band pass filter, a 50 Hz comb band stop filter to remove power line interference and a 50 Hz FIR high pass filter to remove electrocardiogram artifacts [36,67]. The data were then averaged and integrated over 20 samples for each participant. The 1 s immediately preceding the onset of each stimulus was designated as baseline.

2.6. *Electrocardiogram*

ECG data were collected using a three-lead set-up with Ag/AgCl surface click electrodes (BioPac Inc, EL 503) placed inferior to the right and left clavicle and left 8th rib, as described by BioPac (AcqKnowledge, 4.4). A separate 3-minute baseline was collected prior to the start of part 1 of the experiment and prior to the start of part 2 of the experiment. The data were processed offline and the peak-to-peak R-R intervals were identified using the BioPac event-related analysis routine. The data were then visually inspected on a participant-by-participant basis to correct for missing heartbeats or multiple peak identifications. Artifacts and multiple peaks were cross-referenced to the raw ECG file and deleted as appropriate. In the rare case of missing peaks, the R peak was manually inserted into the correct position, as described by the [51]. The R-R intervals were saved as a tachogram and exported to Kubios Standard 3.1.0 [Kubios Oy, Kuopio, Finland [50]] for further data analysis. The primary measure of interest was the root mean square of successive R-R interval differences (RMSSD) analyzed in the time-domain [47].

2.7. *Data analysis*

The RMSSD is recommended for investigations of short time-periods [47]. The RMSSD reflects the beat-to-beat variance in heart rate and is used to estimate vagally-induced changes in HRV. The RMSSD was analyzed in bins of 3 min, to assess how the HRV changed during the session.

2.7.1. *Data pre-processing*

One trial was defined as containing a stimulus presentation (3.3 s) and the subsequent rating by the participant. The facial EMG data were baseline-corrected by subtracting the 1 s immediately preceding the start of a trial from the raw EMG during the touch. Visual inspection showed violations of normal distribution of the facial EMG data. Therefore, the facial EMG residuals were categorized into standard deviation units (i.e. distributed around a mean of 0 with a standard deviation of 1). Thereafter, values outside the ± 2.58 standard deviations were defined as outliers and excluded from the analysis, as described by Field, [17]. In total, ~ 5% of the group facial EMG trials were removed.

Each participant's ECG tachogram was analyzed in Kubios HRV Standard 3.1.0 [Kubios Oy, Kuopio, Finland] [50] and visually inspected to verify that they were normally distributed. To calculate the RMSSD, the tachogram was split into time bins of three minutes (see below). Four tachograms from the first session and two tachograms from the second session were artifactual and could not be analyzed in Kubios. These datasets were removed from the statistical analyses. The data of the three pregnant participants were scrutinized because pregnancy has been reported to affect several cardiac measures, including HRV [e.g. Stein et al. [48]]. One of these subjects had RMSSD values that were outside of the mean ± 2x SD in both sessions. Consequently, the participant's RMSSD data were not analyzed any further.

For the touch investigations (part 1), data from 43 participants were used for the ECG analysis for session 1, and from 44 participants for session 2 (one participant canceled the second session due to illness). The pleasantness and facial EMG analyses were based on responses from 48 participants for session 1, and from 47 participants for session 2. For the comparisons between the touch and odor responses (part 2), the pleasantness ratings, facial EMG responses and ECG responses from 36 participants were included.

2.7.2. *Statistical analysis*

In order to investigate how pleasantness ratings, facial EMG and HRV responses changed during the course of the experiments, linear mixed models were performed. In part 1, pleasantness ratings, corrugator and zygomaticus activity and RMSSD served as dependent variables. Separate analyses were run for each dependent variable. In the analysis of pleasantness, corrugator and zygomaticus activity, “Session” with 2 levels (session 1, session 2) and “Trial” as a continuous covariate were included in the model as fixed factors. To investigate whether the slope of the regression line (“Trial”) differed between session 1 and session 2, an interaction term between “Session” and “Trial” was added to the model. Significant interactions involving the factor “Session” were followed up by separately interpreting and reporting the slopes for session 1 and 2 across trials.

In the analyses of RMSSD, “Session” and “Bins” (11 levels: [baseline + 10 three-minute bins] as a continuous covariate) served as fixed factors. Similarly, the interaction term was included to test for differences in “Session” over “Bins”.

In part 2, the responses to 30 trials of tactile stimulation were compared to the responses to 30 trials of odorant stimulation from the same participant and the same session. In the analysis of ratings, corrugator activity and zygomaticus activity, “Modality” (2 levels: [touch and odor]), and “Trial” as a continuous covariate together with their interaction term were included as fixed factors in the model. In the analyses of RMSSD, “Bins” (6 levels: [baseline + 5 three-minute bins]) and “Modality” (2 levels: [touch and odor]) and their interaction effect served as fixed factors. In all the mixed models, “Subjects” was included as random intercept and “Trial” as random slope to take into account the dependency in the data. Further, the statistical model for the analyses was built according to the principles described by Bolker et al. [4]. Specifically, residuals were plotted and inspected and found to display a normal distribution. Then, Bayesian Information Criteria (BIC) was used to choose the covariance structure, evident by a reduction in BIC value of minimum 2. In the analyses of pleasantness and facial EMG an unstructured covariance type was used, while in the RMSSD analyses, scaled identity was used as covariance type to ensure convergence of the model.

Effect sizes were calculated according to Edwards, Muller, Wolfinger, Qaqish, and Schabenberger [14]. Specifically, the “semi-partial R^2” refers to the relationship between the degrees of freedom numerator, degrees of freedom denominator and the F-value. The effect sizes are thus expressed and interpreted as a semi-partial R^2 of 0.02 indicating a small effect, a semi-partial R^2 of 0.13 indicating a medium effect, and a semi-partial R^2 of 0.26 indicating a large effect [40]. The data were analyzed using SPSS version 25.0 (IBM Corp., NY, USA).

3. Results

Part 1: Touch responses

3.1. *Pleasantness ratings*

The perceived pleasantness of the tactile stimulation dropped significantly across trials in both sessions (Fig. 3, top left), as shown by a main effect of “Trial” (F (1, 47) = 11.523, p = 0.001 [semi-partial R^2 = 0.1969). Pleasantness ratings in session 1 and session 2 were similar at the start of the session, as the main effect of “Session” was not significant (F (1, 5596) = 2.335, p = 0.127) [semi-partial R^2 = 0.0004). The pleasantness ratings changed differently across the subsequent trials during the two sessions. This was evident from a significant

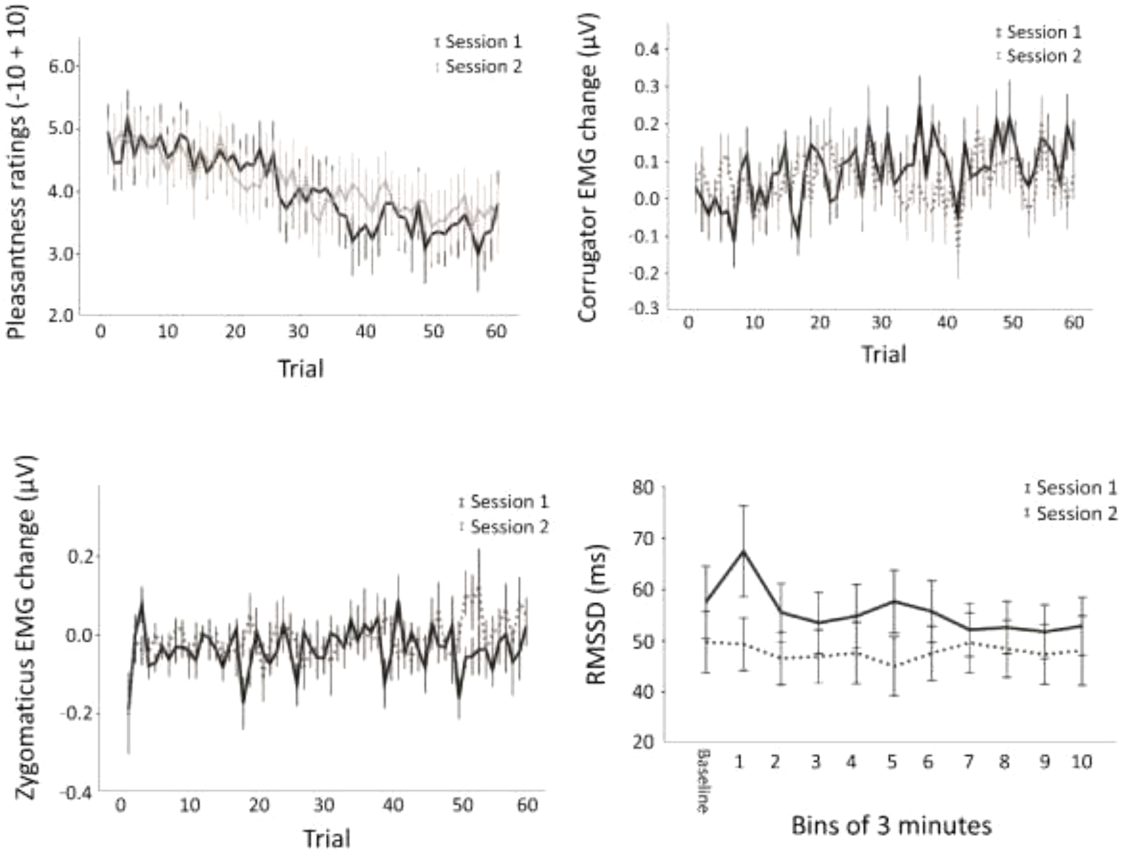

Fig. 3. Top left: Mean pleasantness ratings with SEM. Pleasantness ratings in response to pleasant touch dropped gradually as the sessions progressed and were not significantly different in session 1 and 2. Top right: Mean corrugator activity with SEM. The corrugator activity in response to pleasant touch increased during the first session (full line). Bottom left: Mean zygomaticus activity with SEM. The zygomaticus remained largely unchanged in response to pleasant touch. Bottom right: RMSSD with SEM. The RMSSD remained higher during session 1 than during session 2. However, the RMSSD did not increase significantly from baseline in either session.

Table 1

Interaction effects from linear mixed model with pleasantness ratings, corrugator and zygomaticus activity as dependent variables. Legends: VAS; visual analogue scale (-10 + 10), SE, standard error of the mean, dfd; degrees of freedom denominator, X; interaction between "Session" and "Trial". Trials Session 1: effect of trials in session 1, Trials Session 2: effect of trials in session 2.

		Coefficient	SE	Dfd	T	P
a	Session X Trial	0.009	0.003	5598	−2.66	**0.008**
Pleasantness ratings (VAS)	Trials Session 1	−0.031	0.01	51	−3.86	**0.001**
	Trials Session 2	−0.022	0.008	51	−2.79	**0.007**
b	Session X Trial	0.0023	0.001	5601	3.21	**0.001**
Corrugator activity (µV)	Trials Session 1	0.0024	0.001	107	3.99	**0.001**
	Trials Session 2	0.0001	0.001	107	0.23	0.817
c	Session X Trial	0.0009	0.0005	5546	1.759	0.079
Zygomaticus activity (µV)	Trials Session 1	0.0004	0.0001	71	0.734	0.466
	Trials Session 2	0.0013	0.0005	72	2.309	**0.024**

interaction between "Session" and "Trial" (F (1, 5598) = 7.071, $p = 0.008$ [semi-partial R^2 0.0013], for statistical overview, see Table 1a. The drop in pleasantness ratings was slightly steeper during session 1 than during session 2. For every trial, the pleasantness ratings dropped on a VAS by 0.031 units during session 1 ($p = 0.001$) and by 0.022 units during session 2 ($p = 0.007$).

3.2.1. Facial EMG; corrugator

The corrugator activity increased slightly during both sessions, but the main change occurred during session 1 (see Fig. 3, top right). There was a significant main effect of "Trial" (F (1, 47) = 6.718, $p = 0.013$), [semi-partial $R^2 = 0.13$]), no significant main effect of "Session" (F (1, 5596) = 3.214, $p = 0.073$), [semi-partial $R^2 = 0.0006$]), and a significant interaction between "Session" and "Trial" (F (1, 5601) = 10.287, $p = 0.001$) [semi-partial $R^2 = 0.018$], for statistical overview, see Table 1b). Thus, corrugator activity was similar at the start of the sessions, but developed differently across trials in session 1 and 2. In particular, the corrugator activity only increased significantly during session 1, but not during session 2. Specifically, for every trial, the corrugator increased by 0.0024 µV during session 1 ($p = 0.001$) and 0.0001 µV during session 2 ($p = 0.817$), which indicates that the main effect of "Trial" was driven by session 1.

3.2.2. Facial EMG; zygomaticus

In contrast to the corrugator, the zygomaticus activity remained largely unchanged throughout both sessions (Fig. 3, bottom left). There was no significant main effect of "Trial" (F (1, 46) = 2.909, $p = 0.095$ [semi-partial $R^2 = 0.0595$]), nor a main effect of "Session" (F (1,

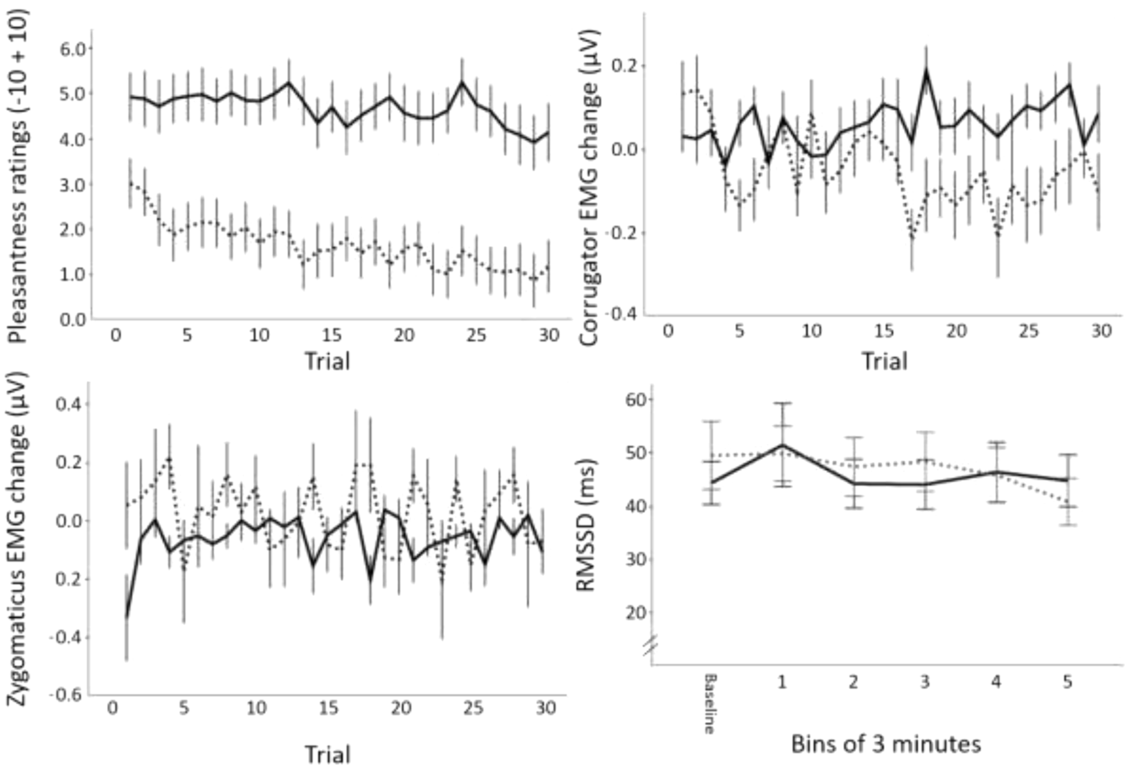

Fig. 4. Top left: Mean pleasantness ratings with SEM. Touch was rated as significantly more pleasant than odor and the ratings decreased less as the session progressed. Top right: Mean corrugator activity with SEM. The corrugator responses decreased for odor, but remained unchanged for touch. Bottom left: Mean zygomaticus activity with SEM. The zygomaticus responses to tactile input was significantly lower than to odor input. Bottom right: RMSSD with SEM. The RMSSD did not increase significantly from baseline in either modality. (Full line, touch condition, dotted line, odor condition).

5546) = 0.006, p = 0.938) [semi-partial R^2 = 0.0001), nor any interaction between "Session" and "Trial" (F (1, 5546) = 3.095, p = 0.079) [semi-partial R^2 = 0.0006]), for statistical overview, see Table 1c.

3.3. Heart rate variability

The RMSSD was overall significantly higher during session 1 than during session 2 (F (1, 679) = 43.036, p = 0.001), [semi-partial R^2= 0.0596]. However, there was no significant main effect of "Bins" on RMSSD (F (10, 753) = 0.694, p = 0.731) [semi-partial R^2= 0.0091], indicating that the RMSSD did not increase during the sessions compared to baseline. There was no interaction between "Session" and "Bins" (F (10, 686) = 1.093, p = 0.365) [semi-partial R^2= 0.0157], see Fig. 3, bottom right.

Part 2: Comparison of touch and odor responses in 30 trials

The main effect of "Trial" shows that the pleasantness ratings decreased significantly (F (1, 35) = 6.367, p = 0.016) [semi-partial R^2 = 0.1539], see Fig 4). Touch pleasantness ratings were significantly higher than odor ratings at the start of the session, evident by a significant main effect of "Modality", (F (1, 2068) = 124.100, p = 0.001) [semi-partial R^2 = 0.0566]. In addition, the ratings changed differently for the two modalities as the trials progressed. This was evident from a significant interaction between "Modality" and "Trial" (F (1, 2071) = 4.660, p = 0.031) [semi-partial R^2 = 0.0023], for statistical overview, see Table 2a. Whereas odor ratings dropped significantly by 0.053 units for every trial (p = 0.003), touch pleasantness ratings dropped by 0.024 units, but non-significantly, for every trial (p = 0.149).

Regarding the comparison of the facial EMG responses, the main effect of "Trial" shows that the corrugator increased by 0.0029 µV per trial (F (1, 35) = 0.951, p = 0.336) [semi-partial R^2 = 0.0265], see Fig 4. At the start of the session, the corrugator activity was similar during touch and odor presentation, evident by a non-significant main effect of "Modality" (F (1, 1999) = 0.285, p = 0.593) [semi-partial R^2 = 0.0001]. However, corrugator activity changed differently for the two modalities during the subsequent trials. This was evident by a significant interaction between "Modality" and "Trial" (F (1, 2006) = 18.882, p = 0.001) [semi-partial R^2 = 0.0093], for statistical overview, see Fig 4 and Table 2b. Specifically, during odor presentation corrugator activity decreased significantly by −0.0055 µV per trial (p = 0.001). During touch, corrugator activity increased slightly, but not significantly across trials (increased by 0.0029 µV per trial; p = 0.086)

The zygomaticus activity did not change during the touch and odor presentation as there was no significant effect of "Trial" (F (1, 35) = 0.097, p = 0.757) [semi-partial R^2 = 0.0028], see Fig 4. However, the zygomaticus activity was significantly lower during the touch than during odor presentation during all trials, as there was a significant main effect of "Modality" (F (1, 2045) = 7.171, p = 0.007) [semi-partial R^2 = 0.0035]. There was no significant interaction between "Modality" and "Trial" (F (1, 2052) = 1.370, p = 0.242) [semi-partial R^2 = 0.0007], for statistical overview, see Fig 4 and Table 2c.

Lastly, the RMSSD responses were not different between odor and touch, as there was no main effect of "Modality" (F (1, 239) = 1.309, p = 0.254) [semi-partial R^2= 0.0055], see Fig 4, bottom right. There was no significant main effect of "Bins" (F (5, 264) = 0.580, p = 0.715) [semi-partial R^2= 0.0108], nor any significant interaction between "Modality" and "Bins" (F (5, 238) = 0.901, p = 0.481) [semi-partial R^2= 0.0186].

4. Discussion

We aimed to investigate the correspondence between subjective and physiological responses to repeated gentle stroking touch by using subjective ratings, facial EMG and heart rate variability responses. In

Table 2
Interaction effects from linear mixed model with pleasantness ratings, corrugator and zygomaticus activity as dependent variables. VAS; visual analogue scale (-10 + 10), SE; standard error of the mean, dfd; degrees of freedom denominator, X; interaction between “Modality” and “Trial”, Trials Touch; effect of trials for touch, Trials Odor; effect of trials for odor.

		Coefficient	SE	Dfd	T	p
a	Modality X Trial	−0.029	0.013	2071	−2.16	**0.031**
Pleasantness ratings (VAS)	Trials Touch	−0.024	0.017	48	−1.47	0.149
	Trials Odor	−0.053	0.017	49	−3.17	**0.003**
b	Modality X Trial	0.0083	0.002	2006	4.338	**0.001**
Corrugator activity (µV)	Trials Touch	0.0029	0.002	78	1.736	0.086
	Trials Odor	−0.0055	0.002	79	−3.300	**0.001**
c	Modality X Trial	0.0035	0.0030	2052	1.171	0.242
Zygomaticus activity (µV)	Trials Touch	0.0011	0.0027	72	0.394	0.695
	Trials Odor	−0.0024	0.0027	73	0.909	0.366

line with previous studies, subjective pleasantness ratings decreased steadily and significantly with repeated exposure to gentle touch. The reduction of the subjective pleasantness ratings across trials was accompanied by a concomitant increase in the corrugator activity. However, the change in perceived pleasantness of the gentle touch was not reciprocated by changes in the zygomaticus muscle or in the heart rate variability. When comparing the touch responses to those elicited by smelling a pleasant odorant, touch was consistently rated as more pleasant than the odorant, but the zygomaticus activity was lower during the touch trials than during the odor trials. However, the drop in pleasantness ratings was more pronounced for the odor responses and was also accompanied by a gradual reduction in corrugator activity. Moreover, we sought to identify consistent response patterns by examining the participants at a second session with an identical set-up. We found that the subjective pleasantness ratings to repeated touch were similar during both sessions, but dropped quicker during session 1. The corrugator activity, however, only increased during the first session, and not during the second session. Whilst the zygomaticus remained largely unchanged during both sessions, the heart rate variability was significantly higher during the first session, but did not change from baseline.

4.1. Pleasantness ratings

Our hypothesis that subjective pleasantness ratings drop with prolonged stimulation was confirmed. The drop is commonly interpreted as a slow “touch satiety” [55]. In contrast to that study, where repeated brush-stroking was applied by a robot [55], pleasantness ratings in the present study remained at a rather high level even towards the end of the session. This may indicate that skin-to-skin touch is more robust to habituation than brush-stroking and could reflect a greater ecological validity of skin-to-skin touch, as suggested by Kress et al. [26]. However, comparisons across the two studies should be interpreted cautiously due to differences in methodology.

4.2. Facial EMG

We believe there is partial support for our second hypothesis: Specifically, we predicted that a drop in subjective ratings would be accompanied by physiological adjustments that indicate changes in positive and negative affect towards the gentle touch. During the first session, the reduction in pleasantness ratings coincided with increased activity in the corrugator muscle, indicating a physiological response that reciprocated the subjective response. Specifically, at the start of the session, the touch was reported to be most pleasant and evoked lowest corrugator activity, and at the end, the touch was reported to be less pleasant and evoked highest overall corrugator activity. In line with our findings, Larsen, Norris, and Cacioppo [29] proposed that the corrugator responds in a linear manner across the affective spectrum. Specifically, when participants were exposed to pictures, sounds and words, negative affective stimuli led to increased activity and positive affective stimuli led to reduced activity in the corrugator muscle. In the present study, the corrugator activity increased as the pleasantness ratings dropped during the first session only. The difference in corrugator activity during session 1 and 2 might reflect subtle differences in attention, which has been reported to affect corrugator activity [10]. Attention can be assumed to be lower in session 2 when participants are familiar with the task and setting.

We were unable to demonstrate a change of zygomaticus activity with repeated touch, and consequently, a correspondence between zygomaticus activity with the ratings. Despite that the zygomaticus has been shown to respond to pleasant auditory [6] and visual input [28], at present, two other studies have failed to identify touch-related responses in the zygomaticus muscle [36, 42], As such, these findings contradict the findings of Pawling and colleagues (2017) who reported increased activity in the zygomaticus to slow stroking touch. Three alternative explanations may help to interpret these contradictory results. First, Larsen et al. [29] proposed that the zygomaticus responds in a “J”-shaped manner. That is, stimuli that are either highly pleasant or aversive will activate the zygomaticus, whereas neutral stimuli will not. In the present study, it may be that the slow stroking touch was not sufficiently pleasant or aversive to yield a response in the zygomaticus muscle. Second, in the present study, the participants were shielded from the experimenters, whereas in the study by Pawling et al. [41] the participant was flanked on either side by two experimenters that observed the participant as the VAS rating was provided. Being observed by the experimenter may affect facial EMG responses, as demonstrated in a study where facial EMG responses to pleasant odors were different when the participants were observed by the experimenter compared to when they were alone [24]. Third, in the present study the participants were only evaluating one type of touch, as opposed to the participants in the study by Pawling et al. [41]. Thus, the differences between the present findings and those reported by Pawling et al. [41] might also reflect the inability to make comparative affective responses between different types of stimuli, which has previously been found to affect touch ratings [55].

4.3. HRV

We were unable to identify a coherent response between the HRV and the subjective responses to gentle touch. HRV did not change from baseline during the tactile stimulation period. This was contrary to our hypothesis. An increase in HRV is typically accredited to emotional well-being and an increased resilience to stress responses [22, 34]. One explanation could be that although the participants reported the repeated touch to be pleasant, it was not sufficiently pleasant to instigate an increase in the HRV. A previous study reported an increase in HRV to pleasant touch [57], however, that particular study used a different HRV measure, the standard deviation of N—N intervals (SDNN). The SDNN is commonly recommended for 24 hours’ measurements [51].

For shorter time intervals, the RMSSD is advocated [47]. Thus, the differences in how HRV changes with repeated touch may be due to the measures used. Alternatively, it may be that the contextual settings were affecting the HRV more than the actual stimulus did, as we observed a higher HRV in session 1 than session 2 although the stimulus was the same. Future studies should investigate the clinical relevance of these findings by comparing the effects of pleasant touch on HRV measures to other interventions that have been reported to increase the HRV, such as meditation [27] or exercise [45].

4.4. Touch and odor comparison

Our findings that pertain to the comparison of the touch and odor responses may be interpreted in several different ways: Firstly, the results suggest that the ratings and corrugator activity are specific for the type of stimulation used. Specifically, the greater reduction in pleasantness observed in the odor ratings was accompanied by a decrease in corrugator activity whereas the reduction in touch pleasantness ratings was accompanied by an increase in corrugator activity. Thus, "satiety" appears to develop differently for stimuli of different modalities and their physiological characteristics are different. Previous findings on odorant processing and corrugator activation report that the corrugator decreased as a function of pleasantness when smelling 12 different food-related odors [3]. However, in the present study, the participants were limited to smelling one single odorant that was also not related to food, making the results of these studies not directly comparable. The development of olfactory satiety may depend on the type of odor [12,56,8]. Secondly, these findings demonstrate that the change in responses is not simply due to the passage of time. If it were, we would expect to see a greater activation of the corrugator during the odor trials, which was always undertaken after the touch trials.

4.5. General discussion

The results from the present study demonstrate a coherence between the subjective pleasantness ratings and the corrugator activity responses to gentle touch during the first session. However, the subjective ratings, zygomaticus activity and HRV responses were non-coherent. Physiological and subjective measures may be incoherent because they reflect different aspects of the experience. For instance, the subjective ratings reflect the conscious evaluation of the gentle touch and the cognitive appraisal of the contextual settings. While participants try to achieve consistency in their ratings [60], they cannot deliberately influence their facial muscle activity or HRV in the same way. Therefore, we speculate that the facial EMG responses in particular reflect a "coarser" physiological evaluation of repeatedly being exposed to a gentle touch that is more prone to change from one session to another than the subjective ratings. Another putative reason for the lack of coherence between the subjective and physiological measures may be explained by the "mere-exposure effect" [66]. The "mere-exposure effect" describes that ratings of stimuli that are repeated typically increase first (i.e., become more positive), before they drop with the number of repetitions. This response pattern can be explained by two opposed processes: habituation and boredom [30 5,39]. It may be speculated that physiological responses and subjective ratings each reflect boredom and habituation to a different extent, therefore they develop differently over time. In general, facial EMG and HRV respond on different time scales. Whereas facial EMG reflects instantaneous emotions, HRV may rather reflect long-term processes such as emotion regulation [53,22]. Altogether, our findings indicate that physiological responses are not blueprint read-outs of the subjective responses, and that cognitive and contextual factors might affect the relationship between the subjective and physiological responses.

5. Limitations

Several limitations apply to the current study. This study collected subjective and physiological responses to repeated pleasant touch and odor. Naturally, due to the lengthy nature of the experiment, the participants' responses are prone to change due to several cognitive factors, such as boredom and attention. Such ratings were not collected as we did not want the participants' perception of mood and boredom to interfere with the evaluation of the gentle touch. However, the ratings from session 1 and 2 were similar and we would expect a larger drop in ratings in session 2 if the change was primarily due to boredom or lack of novelty. Nevertheless, we cannot ascertain the extent to which the detected responses represent a genuine effect of the applied sensory stimulus or a general effect, representing novelty and saliency of potentially any pleasant stimulus. Future studies could circumvent this problem by comparing several types of pleasant stimuli applied for fewer trials.

6. Conclusion

This study presents a comprehensive analysis of the dynamics of subjective and physiological responses to repeated gentle touch examined at two separate sessions. Our findings demonstrate that the drop in perceived pleasantness of repeated gentle touch may be reciprocated by a gradually increasing activity of the corrugator muscle. However, although the corrugator muscle appears to be a promising measure of physiological responses to touch satiety, we were unable to demonstrate coherent subjective and physiological responses during both sessions. The zygomaticus muscle activity and the HRV responses did not change in accordance with the subjective ratings and are likely to reflect other processes that occur irrespective of the subjective appraisal of the gentle touch.

Declaration of Competing Interest

None.

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References

[1] AcqKnowledge. (4.4). Software Guide, Biopac Systems Inc. https://www.biopac.com/wp-content/uploads/acqknowledge-4-software-guide.pdf. Date last accessed 19.03.2020.

[2] B.M. Appelhans, L.J. Luecken, Heart rate variability as an index of regulated emotional responding, Rev. General Psychol. 10 (3) (2006) 229–240, https://doi.org/10.1037/1089-2680.10.3.229.

[3] M. Bensafi, C. Rouby, V. Farget, B. Bertrand, M. Vigouroux, A. Holley, Psychophysiological correlates of affects in human olfaction, Neurophysiol. Clin 32 (5) (2002) 326–332, https://doi.org/10.1016/s0987-7053(02)00339-8.

[4] B.M. Bolker, M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H. Stevens, J.S. White, Generalized linear mixed models: a practical guide for ecology and evolution, Trend. Ecol. Evolut. 24 (3) (2009) 127–135, https://doi.org/10.1016/j.tree.2008.10.008.

[5] R.F. Bornstein, P.R. D'Agostino, Stimulus recognition and the mere exposure effect, J. Pers. Soc. Psychol. 63 (4) (1992) 545–552, https://doi.org/10.1037//0022-3514.63.4.545.

[6] M.M. Bradley, P.J. Lang, Affective reactions to acoustic stimuli, Psychophysiology 37 (2) (2000) 204–215, https://doi.org/10.1111/1469-8986.3720204.

[7] J.T. Cacioppo, G.G. Berntson, J.T. Larsen, K.M. Poehlmann, T.A. Ito, The psychophysiology of emotion, in: J.M. Haviland-Jones, M. Lewis (Eds.), Handbook of Emotions, Guilford Press, New York, 2000, pp. 173–191 2nd ed.

[8] W.S. Cain, F. Johnson, Lability of odor pleasantness: influence of mere exposure, Perception 7 (4) (1978) 459–465, https://doi.org/10.1068/p070459.

[9] N. Caruana, G. McArthur, A. Woolgar, J. Brock, Simulating social interactions for the experimental investigation of joint attention, Neurosci. Biobehav. Rev. 74 (Pt A) (2017) 115–125, https://doi.org/10.1016/j.neubiorev.2016.12.022.

[10] B.H. Cohen, R.J. Davidson, J.A. Senulis, C.D. Saron, D.R. Weisman, Muscle tension patterns during auditory attention, Biol. Psychol. 33 (2–3) (1992) 133–156, https://doi.org/10.1016/0301-0511(92)90028-s.

[11] A.S. Cowen, D. Keltner, Self-report captures 27 distinct categories of emotion bridged by continuous gradients, Proceed. Natl. Acad. Sci. USA 114 (38) (2017) E7900–e7909, https://doi.org/10.1073/pnas.1702247114.

[12] S. Delplanque, G. Coppin, L. Bloesch, I. Cayeux, D. Sander, The mere exposure effect depends on an odor's initial pleasantness, Front. Psychol. 6 (2015) 911, https://doi.org/10.3389/fpsyg.2015.00920.

[13] U. Dimberg, Facial reactions to facial expressions, Psychophysiology 19 (6) (1982) 643–647, https://doi.org/10.1111/j.1469-8986.1982.tb02516.x.

[14] L.J. Edwards, K.E. Muller, R.D. Wolfinger, B.F. Qaqish, O. Schabenberger, An R2 statistic for fixed effects in the linear mixed model, Stat. Med. 27 (29) (2008) 6137–6157, https://doi.org/10.1002/sim.3429.

[15] D.M. Ellingsen, J. Wessberg, O. Chelnokova, H. Olausson, B. Laeng, S. Leknes, In touch with your emotions: oxytocin and touch change social impressions while others' facial expressions can alter touch, Psychoneuroendocrinology 39 (2014) 11–20, https://doi.org/10.1016/j.psyneuen.2013.09.017.

[16] G.K. Essick, F. McGlone, C. Dancer, D. Fabricant, Y. Ragin, N. Phillips, S Guest, Quantitative assessment of pleasant touch, Neurosci. Biobehav. Rev. 34 (2) (2010) 192–203, https://doi.org/10.1016/j.neubiorev.2009.02.003.

[17] A. Field, Discovering Statistics Using IBM SPSS Statistics (4th Ed), Sage, 2013.

[18] A.J. Fridlund, J.T. Cacioppo, Guidelines for human electromyographic research, Psychophysiology 23 (5) (1986) 567–589.

[19] A. Gallace, C. Spence, The science of interpersonal touch: an overview, Neurosci. Biobehav. Rev. 34 (2) (2010) 246–259, https://doi.org/10.1016/j.neubiorev.2008.10.004.

[20] V. Gazzola, M.L. Spezio, J.A. Etzel, F. Castelli, R. Adolphs, C. Keysers, Primary somatosensory cortex discriminates affective significance in social touch, Proceed. Natl. Acad. Sci. USA 109 (25) (2012) E1657–E1666, https://doi.org/10.1073/pnas.1113211109.

[21] V.J. Harjunen, M. Spapé, I. Ahmed, G. Jacucci, N. Ravaja, Individual differences in affective touch: behavioral inhibition and gender define how an interpersonal touch is perceived, Pers. Individ. Dif. 107 (2017) 88–95, https://doi.org/10.1016/j.paid.2016.11.047.

[22] J.B. Holzman, D.J. Bridgett, Heart rate variability indices as bio-markers of top-down self-regulatory mechanisms: a meta-analytic review, Neurosci. Biobehav. Rev. 74 (2017) 233–255, https://doi.org/10.1016/j.neubiorev.2016.12.032.

[23] T. Hummel, B. Sekinger, S.R. Wolf, E. Pauli, G. Kobal, 'Sniffin'sticks': olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold, Chem. Senses 22 (1) (1997) 39–52.

[24] L. Jäncke, N. Kaufmann, Facial EMG responses to odors in solitude and with an audience, Chem. Senses 19 (2) (1994) 99–111.

[25] L.P. Kirsch, C. Krahe, N. Blom, L. Crucianelli, V. Moro, P.M. Jenkinson, A. Fotopoulou, Reading the mind in the touch: neurophysiological specificity in the communication of emotions by touch, Neuropsychologia 116 (Pt A) (2018) 136–149, https://doi.org/10.1016/j.neuropsychologia.2017.05.024.

[26] I.U. Kress, L. Minati, S. Ferraro, H.D. Critchley, Direct skin-to-skin vs. indirect touch modulates neural responses to stroking vs. tapping, Neuroreport 22 (13) (2011) 646, https://doi.org/10.1097/WNR.0b013e328349d166.

[27] J.R. Krygier, J.A. Heathers, S. Shahrestani, M. Abbott, J.J. Gross, A.H. Kemp, Mindfulness meditation, well-being, and heart rate variability: a preliminary investigation into the impact of intensive Vipassana meditation, Int. J. Psychophysiol. 89 (3) (2013) 305–313, https://doi.org/10.1016/j.ijpsycho.2013.06.017.

[28] P.J. Lang, M.K. Greenwald, M.M. Bradley, A.O. Hamm, Looking at pictures: affective, facial, visceral, and behavioral reactions, Psychophysiology 30 (3) (1993) 261–273, https://doi.org/10.1111/j.1469-8986.1993.tb03352.x.

[29] J.T. Larsen, C.J. Norris, J.T. Cacioppo, Effects of positive and negative affect on electromyographic activity over zygomaticus major and corrugator supercilii, Psychophysiology 40 (5) (2003) 776–785, https://doi.org/10.1111/1469-8986.00078.

[30] A.M. Leventhal, R.L. Martin, R.W. Seals, E. Tapia, L.P. Rehm, Investigating the dynamics of affect: psychological mechanisms of affective habituation to pleasurable stimuli, Motiv. Emot. 31 (2) (2007) 145–157, https://doi.org/10.1007/s11031-007-9059-8.

[31] L. Lindgren, S. Lehtipalo, O. Winso, M. Karlsson, U. Wiklund, C. Brulin, Touch massage: a pilot study of a complex intervention, Nurs. Crit. Care 18 (6) (2013) 269–277, https://doi.org/10.1111/nicc.12017.

[32] E. Lynar, E. Cvejic, E. Schubert, U. Vollmer-Conna, The joy of heartfelt music: an examination of emotional and physiological responses, Int. J. Psychophysiol. 120 (2017) 118–125, https://doi.org/10.1016/j.ijpsycho.2017.07.012.

[33] L.S. Löken, J. Wessberg, I. Morrison, F. McGlone, H. Olausson, Coding of pleasant touch by unmyelinated afferents in humans, Nat. Neurosci. 12 (5) (2009) 547–548, https://doi.org/10.1038/nn.2312.

[34] M. Mather, J. Thayer, How heart rate variability affects emotion regulation brain networks, Curr. Opin. Behav. Sci. 19 (2018) 98–104, https://doi.org/10.1016/j.cobeha.2017.12.017.

[35] I.B. Mauss, M.D. Robinson, Measures of emotion: a review, Cognit. Emot. 23 (2) (2009) 209–237, https://doi.org/10.1080/02699930802204677.

[36] L.M. Mayo, J. Linde, H. Olausson, M. Heilig, I. Morrison, Putting a good face on touch: facial expression reflects the affective valence of caress-like touch across modalities, Biol. Psychol. 137 (2018) 83–90, https://doi.org/10.1016/j.biopsycho.2018.07.001.

[37] F. McGlone, H. Olausson, J. Boyle, M. Jones-Gotman, C. Dancer, S. Guest, G. Essick, Touching and feeling: differences in pleasant touch processing between glabrous and hairy skin in humans, Eur. J. Neurosci. 35 (11) (2012) 1782–1788.

[38] W. Mendes, Emotion and the Autonomic Nervous System, in: L.F. Barrett, M. Lewis, J.M Haviland-Jones (Eds.), Handbook of Emotions, Guilford Publications, 2016, pp. 166–181 4th ed..

[39] R.M. Montoya, R.S. Horton, J.L. Vevea, M. Citkowicz, E.A. Lauber, A re-examination of the mere exposure effect: the influence of repeated exposure on recognition, familiarity, and liking, Psychol. Bull. 143 (5) (2017) 459–498, https://doi.org/10.1037/bul0000085.

[40] E. Page-Gould, Multilevel modeling, in: J.T. Cacioppo, L.G. Tassinary, G.G. Berntson (Eds.), The Handbook of Psychophysiology, Cambridge University Press, Cambridge, 2016, pp. 662–678 4th ed.

[41] R. Pawling, P.R. Cannon, F.P. McGlone, S.C. Walker, C-tactile afferent stimulating touch carries a positive affective value, PLoS ONE 12 (3) (2017) e0173457, , https://doi.org/10.1371/journal.pone.0173457.

[42] A. Ree, L.M. Mayo, S. Leknes, U. Sailer, Touch targeting C-tactile afferent fibers has a unique physiological pattern: a combined electrodermal and facial electromyography study, Biol. Psychol.. (2019), https://doi.org/10.1016/j.biopsycho.2018.11.006.

[43] V. Russo, C. Ottaviani, G.F. Spitoni, Affective touch: a meta-analysis on sex differences, Neurosci. Biobehav. Rev 108 (2019) 445–452, https://doi.org/10.1016/j.neubiorev.2019.09.037.

[44] U. Sailer, C. Triscoli, G. Häggblad, P. Hamilton, H. Olausson, I. Croy, Temporal dynamics of brain activation during 40 min of pleasant touch, Neuroimage 139 (2016) 360–367, https://doi.org/10.1016/j.neuroimage.2016.06.031.

[45] G.R. Sandercock, P.D. Bromley, D.A. Brodie, Effects of exercise on heart rate variability: inferences from meta-analysis, Med. Sci. Sport. Exerc. 37 (3) (2005) 433–439, https://doi.org/10.1249/01.MSS.0000155388.39002.9D.

[46] L. Schilbach, B. Timmermans, V. Reddy, A. Costall, G. Bente, T. Schlicht, K. Vogeley, Toward a second-person neuroscience, Behav. Brain Sci. 36 (4) (2013) 393–414, https://doi.org/10.1017/s0140525x12000660.

[47] F. Shaffer, J.P. Ginsberg, An Overview of Heart Rate Variability Metrics and Norms, Front. Public Health 5 (2017) 258, https://doi.org/10.3389/fpubh.2017.00258.

[48] P.K. Stein, M.T. Hagley, P.L. Cole, P.P. Domitrovich, R.E. Kleiger, J.N. Rottman, Changes in 24-hour heart rate variability during normal pregnancy, Am. J. Obstet. Gynecol. 180 (4) (1999) 978–985 0.1016/S0002-9378(99)70670-8.

[49] T. Strauss, R. Kampe, J.P. Hamilton, H. Olausson, F. Rottstadt, C. Raue, I. Croy, Deactivation of default mode network during touch, Sci. Rep. 9 (1) (2019) 1293, https://doi.org/10.1038/s41598-018-37597-1.

[50] M.P. Tarvainen, J.P. Niskanen, J.A. Lipponen, P.O. Ranta-Aho, P.A. Karjalainen, Kubios HRV–heart rate variability analysis software, Comput. Method. Program. Biomed. 113 (1) (2014) 210–220, https://doi.org/10.1016/j.cmpb.2013.07.024.

[51] Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology, Standards of measurement, physiological interpretation, and clinical use, Circulation 93 (5) (1996) 1043–1065.

[52] L.G Tassinary, J.T. Cacioppo, E. Vanman, The Somatic System, in: J.T. Cacioppo, L.G. Tassinary, G.G. Berntson (Eds.), The Handbook of Psychophysiology, Cambridge University Press, Cambridge, 2016, pp. 151–182 4th ed..

[53] 3rd, J.F. Thayer, F. Ahs, M. Fredrikson, J.J. Sollers, T.D. Wager, A meta-analysis of heart rate variability and neuroimaging studies: implications for heart rate variability as a marker of stress and health, Neurosci. Biobehav. Rev. 36 (2) (2012) 747–756, https://doi.org/10.1016/j.neubiorev.2011.11.009.

[54] S.P. Tipper, D. Lloyd, B. Shorland, C. Dancer, L.A. Howard, F. McGlone, Vision influences tactile perception without proprioceptive orienting, Neuroreport 9 (8) (1998) 1741–1744, https://doi.org/10.1097/00001756-199806010-00013.

[55] C. Triscoli, R. Ackerley, U. Sailer, Touch satiety: differential effects of stroking velocity on liking and wanting touch over repetitions, PLoS ONE 9 (11) (2014) e113425, , https://doi.org/10.1371/journal.pone.0113425.

[56] C. Triscoli, I. Croy, H. Olausson, U. Sailer, Liking and wanting pleasant odors: different effects of repetitive exposure in men and women, Front. Psychol. 5 (2014) 526, https://doi.org/10.3389/fpsyg.2014.00526.

[57] C. Triscoli, I. Croy, H. Olausson, U. Sailer, Touch between romantic partners: being stroked is more pleasant than stroking and decelerates heart rate, Physiol. Behav. 177 (2017) 169–175, https://doi.org/10.1016/j.physbeh.2017.05.006.

[58] C. Triscoli, I. Croy, S. Steudte-Schmiedgen, H. Olausson, U. Sailer, Heart rate variability is enhanced by long-lasting pleasant touch at CT-optimized velocity, Biol. Psychol. 128 (2017) 71–81, https://doi.org/10.1016/j.biopsycho.2017.07.007.

[59] E.J. Vanman, B.Y. Paul, T.A. Ito, N. Miller, The modern face of prejudice and structural features that moderate the effect of cooperation on affect, J. Pers. Soc. Psychol. 73 (5) (1997) 941–959.

[60] R.B. Wallace, F.J. Kohout, P.L. Colsher, Observations on interviews surveys of the oldest old, in: R.M. Suzman, D.P. Willis, K.G. Manton (Eds.), The Oldest Old, Oxford, New York, 1992, pp. 123–135 UP, 1992. Print.

[61] I. Wallrabenstein, J. Gerber, S. Rasche, I. Croy, S. Kurtenbach, T. Hummel, H. Hatt, The smelling of Hedione results in sex-differentiated human brain activity, Neuroimage 113 (2015) 365–373, https://doi.org/10.1016/j.neuroimage.2015.03.029.

[62] Westfall, J. (2016). PANGEA: power analysis for general anova designs. https://jakewestfall.shinyapps.io/pangea/. Date last accessed 19.03.2020.

[63] J. Westfall, D.A. Kenny, C.M. Judd, Statistical power and optimal design in experiments in which samples of participants respond to samples of stimuli, J. Exper. Psychol. Gen. 143 (5) (2014) 2020–2045, https://doi.org/10.1037/xge0000014.

[64] M. Wijaya, D. Lau, S. Horrocks, F. McGlone, H. Ling, A. Schirmer, The human "feel" of touch contributes to its perceived pleasantness, J. Exp. Psychol. Hum. Percept. Perform. 46 (2) (2020) 155–171, https://doi.org/10.1037/xhp0000705.

[65] P. Winkielman, K.C. Berridge, Unconscious emotion, Curr. Dir. Psychol. Sci. 13 (3) (2004) 120–123, https://doi.org/10.1111/j.0963-7214.2004.00288.x.

[66] R.B. Zajonc, Attitudinal effects of mere exposure, J. Pers. Soc. Psychol. 9 (2, Pt.2) (1968) 1–27, https://doi.org/10.1037/h0025848.

[67] P. Zhou, B. Lock, T.A. Kuiken, Real time ECG artifact removal for myoelectric prosthesis control, Physiol. Meas. 28 (4) (2007) 397–413, https://doi.org/10.1088/0967-3334/28/4/006.