Somatosensory evoked potentials reveal reduced embodiment of emotions in autism

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Conflict of interest

The authors declare no conflict of interest.

Abstract

Consistent with current models of embodied emotions, this study investigates whether the somatosensory system shows reduced sensitivity to facial emotional expressions in autistic compared to neurotypical individuals, and if these differences are independent from between-group differences in visual processing of facial stimuli. To investigate the dynamics of somatosensory activity over and above visual carryover effects, we recorded EEG activity from two groups of Autism Spectrum Disorder (ASD) or Typically Developing (TD) humans (male and female), while they were performing a facial emotion discrimination task and a control gender task. To probe the state of the somatosensory system during face processing, in 50% of trials we evoked somatosensory activity by delivering task-irrelevant tactile taps on participants' index finger, 105 ms after visual stimulus onset. Importantly, we isolated somatosensory from concurrent visual activity by subtracting visual responses from activity evoked by somatosensory and visual stimuli. Results revealed significant task-dependent group differences in mid-latency components of Somatosensory Evoked Potentials (SEPs). ASD participants showed a selective reduction of SEP amplitudes (P100) compared to TD during emotion task, and TD, but not ASD, showed increased somatosensory responses during emotion compared to gender discrimination. Interestingly, autistic traits, but not alexithymia, significantly predicted SEP amplitudes evoked during emotion, but not gender, task. Importantly, we did not observe the same pattern of group differences in visual responses. Our study provides direct evidence of reduced recruitment of the somatosensory system during emotion discrimination in ASD and suggests that this effect is not a by-product of differences in visual processing.

Significance Statement

The somatosensory system is involved in embodiment of visually presented facial expressions of emotion. Despite autism being characterised by difficulties in emotion-related processing, no studies have addressed whether this extends to embodied representations of others' emotions. By dissociating somatosensory activity from visual evoked potentials, we provide the first evidence of reduced recruitment of the somatosensory system during emotion discrimination in autistic participants, independently from differences in visual processing between typically developing and ASD participants. Our study employs a novel methodology to reveal the neural dynamics underlying difficulties in emotion recognition in ASD and provides direct evidence that embodied simulation of others' emotional expressions operates differently in autistic individuals.

Introduction

Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder characterised by differences in processing social and sensory information and by repetitive patterns of interests and behaviours (American Psychiatric Association, 2013). Within social perception, autistic individuals often demonstrate difficulties in facial emotion recognition (Harms et al., 2010; Gaigg, 2012; Uljarevic & Hamilton, 2013; Loth et al., 2018, but see Bird & Cook, 2013), which has been associated with reduced sensitivity to emotional expressions in visual cortices (Dawson et al., 2005; Deeley et al., 2007; Apicella et al., 2013; Black et al., 2017; Martínez et al., 2019).

Studies in Typically Developing (TD) individuals suggest that beyond the visual analysis of faces, perceiving emotional expressions triggers embodied resonance (Sinigaglia & Gallese, 2018) in sensorimotor regions, which implies re-enacting the visceral, somatic, proprioceptive and motor patterns associated with the observed expressions (Goldman & Sripada, 2005; Hennenlotter et al., 2005; Heberlein & Adolphs, 2007; Niedenthal, 2007; Keysers & Gazzola, 2009, 2010). Research using TMS (Pourtois et al., 2004; Pitcher et al., 2008) and lesion methods (Adolphs et al., 1996, 2000; Atkinson and Adolphs, 2011) have also demonstrated a causal role of the right somatosensory cortex in facial emotion recognition. Importantly, EEG studies directly measuring Somatosensory Cortex (SCx) activity disentangling Visual and Somatosensory Evoked Potentials (V/SEP), have shown SCx engagement in facial emotion recognition over and above any visual carry-over activity (Sel et al., 2014; Sel et al., 2020), providing neural evidence of embodiment of emotional expressions beyond the visual analysis of emotions.

These embodied simulative mechanisms operate differently in ASD. FMRI studies comparing autistic and TD individuals have shown reduced embodied resonance of vicarious affective

touch in the SCx (Masson et al., 2019), and decreased activity in the Premotor Cortex, the Amygdala and the Inferior Frontal Gyrus during perception of dynamic bodily emotional expressions (Grèzes et al., 2008). In another TMS study, ASD participants showed significantly reduced modulations of Motor Evoked Potentials (MEP) during observation of painful stimuli delivered to someone's hand (Minio-Paluello et al., 2009). Together with studies suggesting reduced mirror activity in autistic individuals during observation and imitation of actions (Oberman et al., 2005, 2008) and emotional expressions (Dapretto et al., 2006; Greimel et al. 2010), the evidence suggests that some of the differences in social-emotional cognition characterising ASD are related to reduced simulation of observed actions and feelings. However, the specific processes involved remain the topic of debate, partly because of methodological challenges in dissociating the multiple neural underpinnings of the perception and understanding of other's emotional expressions, such as visual and sensorimotor cortices (see Galvez-Pol et al., 2020).

This study aims to investigate whether emotion processing in ASD is associated with reduced somatosensory activations, over and above differences in visual responses. To this aim, we recorded simultaneous visual and somatosensory evoked potentials by means of electroencephalography (EEG) in two groups of autistic individuals and matched TD controls during a visual emotion discrimination task and a control task, requiring participants to judge either the emotion or the gender of the same facial stimuli. Importantly, we directly measured somatosensory activity by evoking task-irrelevant SEPs (Auksztulewicz et al., 2012) in 50% of trials during the visual tasks. Based on previous research, we used a subtractive method to isolate somatosensory responses from visual carry-over effects (Dell'acqua et al., 2003; Sel et al., 2014; Arslanova et al., 2019; Sel et al., 2020; Galvez-Pol et al., 2018a, 2018b, 2020), thus directly probing the dynamics of somatosensory activity during discrimination of emotional expressions. Moreover, we explored how differences in embodiment of emotional expressions

relate to autistic traits, and measures of alexithymia and interoceptive awareness, which have been argued to contribute to emotion processing differences in autism (Bird & Cook, 2013, Garfinkel et al., 2016). We predicted to observe decreased modulations of SEP amplitudes (free from visual activity) in ASD compared to TD, reflecting reduced embodiment of emotional expressions in autistic individuals.

Materials and Methods

Participants. Twenty-two adult participants with a diagnosis of Autism Spectrum Disorder (ASD) and twenty-two Typically Developing (TD) adults matched for IQ, age and gender took part in the experiment. Datasets from two participants (1 ASD, 1 TD) were not included in the final analyses because stimulus markers were accidentally not recorded during data collection. We excluded two additional ASD participants because of excessive artefacts in the EEG data (drift due to sweat and artefacts caused by muscular tension) and two TD participants because they scored above cut off on the Social Responsiveness Scale (SRS-2) and Autism Quotient (AQ) respectively. We ensured that there was no significant difference in artefact rejection between the two groups. The final sample was thus composed of 19 ASD (17 right handed, 1 female, mean age 40.47 ± 8.87) and 19 TD participants (19 right handed, 1 female, mean age 40.84 ± 12.25). The sample size was extracted from a study by Sel and colleagues (Sel et al., 2014), adopting a similar paradigm in typically developing participants (n = 16). We ensured to achieve high statistical power by administering a large number of trials per experimental condition, in line with recent literature (Baker et al., 2020, Boudewyn et al., 2018) showing that, in ERP studies, statistical power increases as a function of the interaction between sample size, effect size, and number of trials. Moreover, a post-hoc sensitivity analysis was carried out in GPower (Perugini et al., 2018) to determine the

smallest effect size which could be reliably detected by our Group*Task*Hemisphere*Region*Site*Emotion (2*2*2*3*3*3*3) repeated-measures ANOVA, given our sample size (n = 38), an alpha level of .05, and power of .80. Results highlighted that the smallest detectable effect size was .07, and the critical F was 1.24, confirming the validity of our results.

All participants in the ASD group had a formal diagnosis of autism spectrum disorder from qualified professional clinicians based on the DSM criteria. To control for IQ, we tested all our participants with a short version of the Weschler Adult Intelligence Scale (WAIS), and obtained a Verbal IQ (VIQ) and Performance IQ (PIQ) for each participant. Moreover, participants completed the adult self-report form of the Social Responsiveness Scale (SRS-2; Constantino and Gruber, 2012)), the Autism-Spectrum Quotient (AQ; Baron-Cohen et al., 2001), the Toronto Alexithymia Scale (TAS-20;Bagby et al., 1994)) and the Multidimensional Assessment for Interoceptive Awareness (MAIA–2; Mehling et al., 2018). For a summary of test and questionnaires scores, see Table 1.

Stimuli. We used a set of pictures depicting neutral, fearful and happy emotions used in a previous study (Sel et al., 2014), originally selected from the Karolinska Directed Emotional Faces set (Lundqvist et al., 1998). The grayscaled faces were enclosed in a rectangular frame (140 x 157 inches), excluding most of the hair and non-facial contours.

Task. Participants sat in an electrically shielded chamber (Faraday's cage) in front of a monitor at a distance of 80 cm. Visual stimuli were presented centrally on a black background using E-Prime software (Psychology Software Tools). Trials started with a fixation cross (500 ms), followed by the presentation of a face image (neutral, fearful or happy, either male or female) for 600 ms.

153 The experiment consisted of 1200 randomised trials, presented in two separate blocks of 600
154 trials, which included 200 neutral, 200 fearful and 200 happy faces (half male and half female),
155 presented in random order. In the emotion task (block 1), participants were instructed to attend
156 to the emotional expression of the faces, while in the gender task (block 2) they needed to
157 attend to the gender of the faces. The order of presentation of the two blocks was
158 counterbalanced across participants. To ensure participants were attending to the stimuli, in
159 10% of emotion block trials, participants were asked whether the face stimulus was fearful (Is
160 s/he fearful?) or happy (Is s/he happy?), or whether it depicted a female (Is s/he female?) or
161 male (Is s/he male?) during the gender block trials. When a question was presented, participants
162 had to respond vocally (yes/no) as soon as possible. Responses were recorded with a digital
163 recorder and manually inserted by the experimenter, who was able to hear the participant from
164 outside the Faraday's cage through an intercom. Before starting each block, participants
165 completed a practice session with 12 trials (4 neutral, 4 happy, 4 fearful, half male/female).

166 To evoke SEPs during the task, in 50% of trials (Visual-Tactile Condition; VTC), participants
167 received task-irrelevant tactile taps on their left index finger 105 ms after face images onset
168 (Sel et al., 2014). In the Visual-Only Condition (VOC, 50% of trials), the same visual facial
169 stimuli were presented without any concurrent tactile stimulation (see Figure 1A for an
170 illustration of a trial). VTC and VOC were equally distributed in each block across the stimulus
171 types (emotion, gender).

172 Tactile taps were delivered using two 12 V solenoids driving a metal rod with a blunt conical
173 tip that contacted participants' skin when a current passed through the solenoids. Participants
174 were instructed to ignore the tactile stimuli. To mask sounds made by the tactile stimulators,
175 we provided white noise through one loudspeaker placed 90 cm away from the participants'
176 head and 25 cm to the left side of the participants' midline (65 dB, measured from the
177 participants' head location with respect to the speaker).

After completing the experimental task, every participant completed a brief rating task in which they rated the previously observed expressions from 0 (extremely happy) through 50 (neutral) to 100 (extremely fearful) using a Visual Analogue Scale (VAS). On separate trials they also rated gender from 0 (extremely female) to 100 (extremely male).

EEG recording and data pre-processing. We recorded EEG from a 64 electrodes cap (M10 montage; EasyCap). All electrodes were on-line referenced to the right earlobe and off-line re-referenced to the average of all channels. Vertical and bipolar horizontal electrooculogram and heartbeats were also recorded. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling rate).

Analysis of the EEG data were performed using BrainVision Analyzer software (BrainProducts). The data was digitally low-pass-filtered at 30 Hz and high-pass-filtered at 0.1 Hz. Ocular correction was performed (Gratton et al., 1983) and the EEG signal was epoched into 700 ms segments, starting 100 ms before visual (for VEP analysis) and tactile (for SEP analysis) stimulus onsets. We performed baseline correction using the first 100 ms before stimulus onsets. Artefact rejection was computed eliminating epochs with amplitudes exceeding 100 μV. Single-subject grand-averaged ERPs for each condition (VOC and VTC), task (Emotion, Gender) and emotion (Neutral, Fearful, Happy) were computed. For SEPs, after pre-processing, single-subject averages of VOC trials were subtracted from single-subject averages of VTC trials, in order to isolate somatosensory evoked responses from visual carryover effects (Galvez-Pol et al., 2020). This subtractive method is described in Figure 1B.

Statistical analysis

Accuracy of catch-trials. We extracted the mean accuracy for each participant, expressed in a value in a range between 0 (0% of correct answers) and 1 (100% correct answers). Exclusion criteria was set to accuracy below 50%. We computed a 2x2 frequentist and Bayesian mixed

repeated-measures ANOVA with group (TD, ASD) as a between factor and task (Emotion, Gender) as a within factor.

Visual Analogue Sscale (VAS) ratings. We computed two frequentist and Bayesian mixed repeated-measured ANOVAs for emotion and gender ratings separately. For emotion ratings, factors were group (TD, ASD) as between factor and emotion (Neutral, Fearful, Happy) as within factor. For gender ratings, factors were group (TD, ASD) as between factor and gender (Female, Male) as within factor.

Amplitudes of SEP. We computed mean amplitudes of SEP in four consecutive time windows of 30 ms length starting from 40 ms up to 160 ms after tactile stimulus onset (occurring after 105 ms of visual stimulus onset). These time windows were centred on the P50 (40-70 ms), N80 (70-100 ms), P100 (100-130 ms) and N140 (130-160 ms) peaks (Eimer & Forster, 2005; Bufalari et al., 2007; Schubert et al., 2008). Analyses were restricted to 18 electrodes located over sensorimotor areas (corresponding to FC1/2, FC3/4, FC5/6, C1/2, C3/4, C5/6, Cp1/2, Cp3/4, CP5/6, of the 10/10 system) (Sel et al. 2014). We selected the time windows from the grand average of all conditions and participants (Luck, 2014). SEP mean amplitudes were analysed through mixed repeated-measures ANOVAs in SPSS and JASP. Consistent with previous analyses (Sel et al., 2014), within-group factors of the ANOVAs were: task (Emotion, Gender), emotion (Neutral, Fearful, Happy), hemisphere (Left, Right), site (Dorsal, Dorsolateral, Lateral; i.e., clusters of three electrodes grouped in parallel to the midline), region (Frontal, Central, Posterior; i.e., clusters of three electrodes grouped perpendicularly to the midline) and the between factor group (TD, ASD). Follow-up ANOVAs and two-tailed independent and paired sample t-tests were carried out to follow-up significant interactions, and post-hoc pairwise comparisons were computed on significant main effects. We applied Greenhouse-Geisser when appropriate (Keselman & Rogan, 1980) and post-hoc tests were corrected for multiple comparisons (Bonferroni). In order to evaluate the likelihood of the

experimental hypothesis over the null hypothesis, we ran additional Bayesian statistics in JASP (Caspar et al., 2020). Bayesian repeated-measures ANOVAs were run to test the likelihood of inclusion of specific interaction or main effect (BF_{incl}) across matched models, as recommended in Keysers et al., 2020. Only factors of interest were included to reduce the computational cost of the analyses. Bayesian model comparisons on high-order interactions with ≥ 5 factors could not be computed in JASP because they exceeded the computational capacity of the software, therefore only follow-ups (including ≤ 4 factors) on these interactions were computed. Bayesian independent and paired t-tests were run in JASP (Keysers et al., 2020, van Doorn et al., 2021) to support the experimental hypothesis or to provide evidence of absence of effects (Keysers et al., 2020) over the control condition. In cases where a one-tailed hypothesis was tested, the directionality of the hypothesized effect is indicated as a subscript to the BF (e.g. BF_{+0} for a positive effect, BF_{-0} for a negative effect) (Caspar et al., 2020). Priors were set in accordance with default parameters (Cauchy distribution with a Scale parameter of $r = \sqrt{2/2} \approx 0.707$) to provide an objective reference to our analysis (Keysers et al., 2020), and robustness check was used to test sensitivity of results to changes in prior's features. For H1, a Bayes factor between 1 and 3 is considered anecdotal evidence, a Bayes factor between 3 and 10 is considered moderate evidence, and a Bayes factor greater than 10 is considered strong evidence; for H0, a Bayes factor between 1 and 1/3 is considered anecdotal evidence, a Bayes factor between 1/3 and 1/10 is considered moderate evidence, and a Bayes factor smaller than 1/10 is considered strong evidence (Jeffreys, 1998; Keysers et al., 2020; van Doorn et al., 2021).

Amplitudes of VEP. We used single-subject averages of VEPs on the data corresponding to the visual-only condition and free from any contamination from SEPs. Analyses were computed on 30 ms time windows, centred on the visual components P1 (120-150 ms), N2 (170-200 ms) and P3 (240-270 ms). ERPs were computed at occipital sites (corresponding to O1/2, O9/10,

PO9/10 electrodes of the 10/10 system) (Conty et al., 2012). We selected the time windows from the grand average of all conditions and participants (Luck, 2014). VEP mean amplitudes were analysed through mixed repeated-measures ANOVAs in SPSS, including the factors group (TD, ASD), task (Emotion, Gender) hemisphere (Left, Right), electrode (corresponding to O1/2, O9/10, PO9/10 electrodes of the 10/10 system) and emotion (Neutral, Fearful, Happy). We applied Greenhouse-Geisser correction for non-sphericity when appropriate (Keselman & Rogan, 1980) and post-hoc tests were corrected for multiple comparisons (Bonferroni).

In addition, Bayesian repeated-measures ANOVAs, independent and paired t-tests were run in JASP to evaluate the likelihood of H1 over the null hypothesis or to provide evidence in favour of H0 (Keysers et al., 2020; van Doorn et al., 2021). The parameters used were consistent with SEP analysis.

Correlations and linear regressions between personality traits and SEP and VEP amplitudes

We first ran correlations between questionnaires scores (Social Responsiveness Scale (SRS-2); Autism Quotient (AQ); Toronto Alexithymia Scale (TAS-20); Multidimensional Assessment of Interoceptive Awareness (MAIA-2)) to examine associations between personality traits. Then, we computed correlations in SPSS with the aim to explore linear relationships between autism, alexithymia and interoception, and somatosensory and visual responses to emotional faces. Specifically, we tested if individual scores on questionnaires measuring autistic traits (SRS-2 and AQ), alexithymia (TAS- 20) and interoceptive awareness (MAIA-2) significantly correlated with SEP and VEP amplitudes during emotion and gender tasks. We focused on the SEP and VEP components and clusters of electrodes where significant group effects were found. We first ran correlations on the whole sample, and then on the ASD group only. Then, we ran a multiple linear regression including as predictors of SEPs the scores on the four questionnaires. In addition, Bayesian correlations and linear regressions were

computed in JASP to provide evidence in favour or against our experimental hypotheses. In cases where a one-tailed hypothesis was tested, the directionality of the hypothesized effect is indicated as a subscript to the BF (e.g. BF_{+0} for a positive effect, BF_{-0} for a negative effect) (Caspar et al., 2020).

Source Reconstruction

We performed source reconstruction of SEPs with SPM 12 (Ashburner et al., 2014) using a standard MRI template with the COH – Smooth Priors method (Friston et al., 2008), a source reconstruction method assuming locally coherent and distributed sources (Bonaiuto et al., 2018) equivalent to LORETA (Pascual-Marqui et al., 1994; Pascual-Marqui, 2002). We performed source analysis on segments of 150 ms, 200 ms and 300 ms length, starting from tactile onset. The segments were grand-averaged across subjects (Fogelson et al., 2014; Ranlund et al., 2016) for each group and task. We specified two conditions for each group (Emotion Task and Gender Task) which were source reconstructed separately. After inverting the three models, we selected the model with the highest log-evidence or marginal likelihood (Friston et al., 2008) We extracted the MNI coordinates of the voxel showing the strongest level of activity for each SEP peak of interest (P50: 50 ms; N80: 90 ms; P100: 110 ms; N140: 145 ms) and converted to Brodmann areas with the Atlas Bioimage Suite Web (Papademetris et al., 2006).

Results

Behavioural Performance on Face Emotion and Gender catch trials during EEG recording. The mixed repeated-measures ANOVA showed a significant main effect of group ($F_{(1,36)}$=5.396, $p\eta^2$= .130, p=.026, BF_{incl} = 2.402), explained by an overall decreased accuracy for the ASD (M =88.6%, SD=1.9%) compared to the TD group (M =95.0% SD=1.9%). No

300 further significant effects were found (main effect of task, p=.392, BF_{incl} = .273; Group*Task
301 interaction, p=.185, BF_{incl} = .823), suggesting that the behavioural differences between the two
302 groups were not task-dependent.

303 *Subjective ratings of Emotion and Gender intensity.* Results highlighted a main effect of
304 emotion ($F_{(1.10, 41.77)}$ = 764.861, $p\eta^2$= .955, p<.000, BF_{incl} = 9.603e+68). Bonferroni corrected
305 post-hoc pairwise comparisons showed a significant difference between mean ratings of
306 neutral, fearful and happy expressions (all ps <.001, all BF_{10} > 1.5e+20; neutral: M = 49.389,
307 SD = 2.975; fearful: M = 16.336, SD = 8.415; happy: M = 87.259, SD = 7.797). The two groups
308 did not show statistically significant differences in how they rated the emotional expressions,
309 as highlighted by non-significant Group*Emotion interaction (p=.372, BF_{incl} = .189) and non-
310 significant main effect of group (p=.519, BF_{incl} = .751).

311 Moreover, we found a significant main effect of gender on the pictures ($F_{(1,36)}$ = 915.433, $p\eta^2$=
312 .962, p=.000, BF_{incl} = 1008e+47; female: M = 8.466, SD = 9.410; male: M = 91.995, SD =
313 9.586), highlighting a significant difference in how participants rated pictures displaying
314 female and male individuals. The Task*Group interaction was also significant ($F_{(1,36)}$ = 5.703,
315 $p\eta^2$ = .137, p=.022, BF_{incl} = 18.196). We computed two independent-sample t-tests for female
316 and male faces. Results suggested a significant difference in how TD and ASD rated male
317 (t(26.074) = -2.600, p=.015, Cohen's d = .603, BF_{10} = 3.987; TD: M = 95.76, SD = 5.51; ASD:
318 M = 88.23, SD = 11.34), but not female faces (p=.064, BF_{10} = 1.299).

319

320 ***EEG results***

321 *Somatosensory activity (SEP, VEP free) during emotion and gender visual discrimination task*
322 Somatosensory processing was isolated from concomitant visual activity by subtracting the
323 visual only condition from the visuo-tactile condition (i.e., visual-tactile minus visual-only

trials, see Figure 1B). We only report significant interactions and main effects including the factors of interest (i.e., group, task, emotion). A summary of findings highlighting group differences is provided. For the full report of results and description of each analytical step, see the paragraph 'Full analysis'.

Group differences in somatosensory processing of emotional expressions

The analyses of the early SEP components suggested that, during the N80 SEP component, responses to different emotions varied significantly across sites only in typically developing participants, as shown by the significant Emotion*Site interaction in the TD group ($F_{(2.657, 47.828)}$ = 4.123; $p\eta^2$= .186; p = .014) although this result was not supported by Bayesian statistics (BF_{incl} = .092). In ASD, no interactions or main effects involving the factor emotion were found (all ps >.05, all BF_{incl} < .024).

During the P100 mid-latency SEP component, results indicated enhanced somatosensory responses during emotion discrimination task in the TD compared to the ASD group, particularly in frontal and dorsal regions. This was highlighted by follow-up analyses on significant Group*Task*Region and Group*Task*Site interactions (see the paragraph 'Full analysis'), revealing enhanced somatosensory responses in TD compared to ASD during emotion discrimination in the frontal region by both frequentist and Bayesian statistics (two-tailed independent-sample t-test: t(36) = 2.054, p =.047, Cohen's d = .666, BF_{+0} = 3.049) and the dorsal site (two-tailed independent-sample t-test: t(36) = 2.311, p=.027, Cohen's d = .750, BF_{+0} = 4.675). Moreover, the overall activity during emotion task was enhanced in TD compared to ASD (follow-up on the significant Group*Task interaction: main effect of group in emotion task: $F_{(36, 1)}$ =6.51, $p\eta^2$= .15, p=.015, Bayesian independent-sample t-test: BF_{+0} = 7.21). All these effects were not-significant for gender task (all ps > .395, all BF_{10} < .422). In

addition, in the TD group, follow-up analyses showed that somatosensory responses were significantly enhanced for emotion task compared to gender task in the frontal region (two-tailed paired sample t-test: $t(18) = 2.166$, $p = .044$, Cohen's $d = .497$, $BF_{+0} = 3.044$).). In the ASD group, we found no significant differences between somatosensory responses during emotion and gender task ($p=.171$, $BF_{+0} = .11$). Group differences in the frontal region in SEP P100 are depicted in Figure 2.

Finally, during the N140 SEP component, group differences were primarily apparent in the right hemisphere, where SEP in response to different emotions varied across tasks in the TD but not the ASD group. In fact, in TD, we found a significant Task*Emotion interaction in the right hemisphere ($F_{(2,36)} =3.302$; $p\eta^2=.155$, $p=.048$; however, $BF_{incl} = .11$), while no significant interactions involving the factors task and emotion were found in ASD (all ps >.05, all $BF_{incl} < 1/3$).

Full analysis

Early sensitivity of SEPs to emotional expressions in TD (P50, N80)

P50: Results highlighted a significant interaction between Group*Site*Region ($F_{(3.19,114.94)} =3.026$; $p\eta^2 =.078$; $p =.030$, $BF_{incl} = .008$). We followed-up the Group*Site*Region interaction by performing three mixed repeated-measures ANOVAs for each Region (Frontal, Central, Parietal) and Site (Dorsal, Dorsolateral, Lateral), but no significant interactions involving the factor group emerged from this analysis (all ps > .05, all $BF_{incl} < 1/3$).

In this time window, we also found a significant Task*Emotion*Hemisphere*Site*Region interaction ($F_{(5.82,209.36)} = 2.353$; $p\eta^2 =.06$; $p =.033$). We followed-up this significant interaction computing two separate mixed repeated-measures ANOVAs for emotion and gender tasks. In the emotion task, results showed a significant Emotion*Site*Region interaction ($F_{(8, 896)} =$

3.026; $p\eta^2$ =.076; p=.003), although not supported by Bayesian statistics, (BF_{incl} = .003). To follow-up this interaction, we performed an Emotion*Site repeated-measures ANOVA for each region (frontal, central and posterior). We found a significant Emotion*Site interaction in the frontal region ($F_{(3.363,124.435)}$ = 3.148; $p\eta^2$ =.078; p =.023, BF_{incl} = .085; central and posterior regions, all ps >.05, all BF_{incl} < 1/3) but further follow-up for each site in the frontal region (dorsal, dorsolateral, lateral) did not reveal significantly different responses to emotional expressions (Dorsal Site: p=.264, BF_{incl} = .476; Dorsolateral Site: p=.212, BF_{incl} = .212; Lateral Site: p= .464, BF_{incl} = .078). No significant effects involving the factor emotion were found when the ANOVA was performed in the Gender Task (all ps >.05, all BF_{incl} < 1).

N80: The mixed-repeated measures ANOVA highlighted a significant Group*Emotion*Hemisphere*Site*Region interaction ($F_{(5.26, 189.71)}$ =2.236; $p\eta^2$=.058; p =.049) To follow-up this interaction, we computed two repeated-measures ANOVAs for the ASD and TD groups including the factors emotion, hemisphere, site and region. In the TD group we found a significant cross-over interaction between Emotion*Site ($F_{(2.657, 47.828)}$ = 4.123; $p\eta^2$= .186; p = .014) although BF_{incl} highlighted evidence against the inclusion of this interaction in the model (BF_{incl} = .092). Further follow-up running three separate ANOVAs for dorsal, dorsolateral and lateral sites failed to show statistically significant differences between the three emotions (Dorsal Site: p=.133; Dorsolateral Site: p=.796; Lateral Site: p=.135; all BF_{incl} < 1). No significant interactions involving the factor emotion were found in the ASD group (all ps >.05, all BF_{incl} < .025).

In addition, the main ANOVA yielded a significant Emotion*Site ($F_{(4,140)}$ =5.005; $p\eta^2$ =.122; p=.000, BF_{incl} = .062) interaction. Follow-up analysis on the Emotion*Site interaction revealed a main effect of emotion in the dorsal site (F(2,74) = 4.340, pη2=.104 p=.017, BF_{incl} = 41.056) and Bonferroni post-hoc test highlighted enhanced responses for fearful compared to happy expressions (p=.013, BF_{10} = 6218.018, all other ps >.05, all other BF_{10} < 3).

Task dependent group differences in somatosensory responses (mid latencies P100, N140)

P100: The main ANOVA yielded the following significant interactions involving the between-factor group: Group*Task*Region ($F_{(1.43,\ 51.83)}$ =4.252; $p\eta^2$ =.106, p =.031, BF_{incl} = .120), Group*Task*Site ($F_{(1.38,\ 49.83)}$ = 4.958; $p\eta^2$ = .121, p =.020, BF_{incl} = 6.526), Group*Task ($F_{(1,\ 36)}$ = 4.608; $p\eta^2$ =.113; p=.039, BF_{incl} = 28.937). Conversely, main effects of Group (p= .066, BF_{incl} = .551) and Task (p=.647, BF_{incl} = .046) were not significant.

To understand the Group*Task*Region interaction, three separate Group*Task ANOVAs were carried out for frontal, central and posterior regions. We found a significant Group*Task interaction specific for the frontal region ($F_{(1,36)}$ =6.729, $p\eta^2$=.157, p=.014), confirmed by Bayesian analysis (BF_{incl} = 4.143). We computed an independent-sample t-test which highlighted a significantly enhanced positivity in the TD compared to ASD Group in the emotion task (t(36) =2.054, p =.047, Cohen's d = .666) but not in the gender task (p =.823). Bayesian independent-sample t-tests were in favour of H1 for emotion task (BF_{+0} = 3.049) and of H0 for gender task (BF_{10} = .321) in the frontal region. Moreover, a paired sample t-test revealed a significantly increased positive response in the emotion task compared to the gender task in the TD (t(18) =2.166, p =.044, Cohen's d = .497) but not the ASD Group (p =.171) in the frontal region. Bayesian paired-sample t-test was in favour of H1 in the TD group (BF_{+0} = 3.044) and of H0 (BF_{+0} = .11) in the ASD group. No effects involving group and task were found in the central and posterior regions (all ps >.05, all BF_{incl} < 3).

To follow-up the Group*Task*Site interaction, three mixed repeated-measures ANOVAs for the dorsal, dorsolateral and lateral sites were carried out. This analysis revealed a significant Group*Task interaction specific for the dorsal site (F(1,36) =6.939, $p\eta^2$ =.162, p=.012, BF_{incl} = 4.445), where significant group differences, revealed by independent-sample t-tests, were

found in the emotion task (t(36) =2.311, p=.027, Cohen's d = .750, Bayesian t-test: BF_{+0} = 4.675) but not in gender task (p=.777, Bayesian t-test: BF_{10} = .325). Task comparisons carried out by paired samples t-tests were not significant either in TD and ASD and no significant effects involving task and/or group were found in other sites (all ps >.05, all $BF_{incl} < 3$).

We also computed two separate mixed repeated-measures ANOVAs for emotion and gender task, which revealed a main effect of group in the emotion task ($F_{(36, 1)}$ =6.51, $p\eta^2$ = .15, p=.015; Bayesian independent-sample t-test: BF_{+0} =7.21). No main effect of group (p=.395, BF_{incl} = .422) or interactions involving the factor group (all ps >.05, all $BF_{incl} < 3$) were found in the gender task.

The main ANOVA also yielded an interaction involving the within-factors task and emotion (Task*Emotion*Hemisphere*Site*Region ($F_{(5.52, 198.90)}$ =2.68, $p\eta^2$= .069, p=.018). We followed up this interaction computing two repeated-measures ANOVAs for the emotion and gender tasks, collapsing the between-factor group. Results revealed a significant Emotion*Site*Region interaction specific for the emotion task ($F_{(4.692,173.588)}$ =2.600, $p\eta^2$=.066, p=.030, BF_{incl} = .002), but further follow-up breaking by region and by site did not highlight any significant emotion effect (all ps >.05, all $BF_{incl} < 1/3$). No interactions or main effects involving the factor emotion were found in the gender task (all ps>.05, , all $BF_{incl} < 1/3$).

N140: The analysis revealed a significant Group*Task*Emotion*Hemisphere interaction ($F_{(2,72)}$=4.06; $p\eta^2$=.10, p=.021), confirmed by Bayesian analysis (BF_{incl} = 7.455). To follow-up this interaction, we computed two repeated measures ANOVAs for the TD and ASD groups including the factors task, emotion and hemisphere. In the TD group, results revealed a significant Task*Emotion*Hemisphere interaction ($F_{(2,36)}$ =6.596; $p\eta^2$=.268, p=.004, BF_{incl} = 24.544), explained by a crossover interaction between task and emotion in the right hemisphere ($F_{(2,36)}$ =3.302; $p\eta^2$=.155, p=.048, BF_{incl} = 1.188). Further follow-up on the Task*Emotion

interaction, performed computing two separate repeated measures ANOVAs for emotion and gender tasks, did not show statistically significant differences between the three emotions (all ps >.05, all $BF_{incl} < 3$). In the ASD group, the repeated-measures ANOVA involving the factors task, emotion and hemisphere didn't yield any significant interaction of main effect involving task or emotion (all ps >.05, all $BF_{incl} < 1/3$).

The main ANOVA also yielded a significant Task*Emotion*Hemisphere*Site*Region interaction ($F_{(8,288)}$,=2.09; $p\eta^2$=.05, p=.037). To follow it up, we ran two repeated-measures ANOVAs for emotion and gender tasks separately. Results showed no significant interactions involving the factor emotion in the emotion task (all ps >.05, all $BF_{incl} < 1/3$). A significant Emotion*Hemisphere*Site*Region interaction ($F_{(8,296)}$=2.167; $p\eta^2$=.055, p=.030) was found in the gender task, however, Bayesian statistics highlighted strong evidence against models including this interaction (BF_{incl} = .003). Further follow-up analysis breaking the interaction by hemisphere, site and region did not show significant interactions involving the factor emotion (all ps >.05, all $BF_{incl} < 1/3$).

Linear relationships between personality traits and SEP amplitudes

The correlation analyses among personality traits revealed significant correlations between autistic traits (measured with SRS-2 and AQ), alexithymia (TAS-20) and interoceptive awareness (MAIA-2) in the whole sample of participants (all ps < .02, all BF > 3). Interestingly, in the ASD group, autistic traits and alexithymia were not correlated (all ps > .5; all BF < 1/2), while both SRS-2 and AQ were significantly correlated with MAIA-2 (all ps <. 02, all BF > 3). For a summary of these results, see Table 2A (whole sample) and 2B (ASD group).

We then ran correlations between personality traits and SEP amplitudes. We focused on the P100 component, where significant group differences were highlighted by t-tests. We

computed correlations between participants' scores on Social Responsiveness Scale (SRS-2), Autism Quotient (AQ), Toronto Alexithymia Scale (TAS-20) and Multidimensional Assessment of Interoceptive Awareness (MAIA-2) and mean SEP amplitudes in all the clusters of electrodes where significant between-group differences were found (frontal SEP amplitudes (mean activity of 6 electrodes over frontal sensorimotor regions), mean SEP amplitudes (mean activity of 18 electrodes over sensorimotor regions), dorsal SEP amplitudes (mean activity of 6 electrodes over sensorimotor areas close to the midline). Interestingly, autistic traits measured both by the Social Responsiveness Scale (SRS-2) and the Autism Quotient (AQ) were highly correlated with SEP amplitudes evoked during the emotion task in all clusters of electrodes (all ps <.006, all $BF_{0-} > 18.413$), see Table 3. Conversely, correlation between SRS-2 and AQ scores and somatosensory activity evoked during the gender task was not significant in almost every electrode cluster. These results highlight a strong and persistent relationship between patterns of somatosensory responses evoked during the emotion discrimination task and autistic traits. Interoceptive awareness was also significantly correlated with the activity evoked during the emotion task (all ps <.015, all $BF_{0+} > 8.188$) but not gender task (all ps >.35, all $BF_{0+} < .5$) in all clusters of electrodes. Alexithymia did not show a significant relationship with SEP amplitudes in emotion task (all ps >.120, all $BF_{0-} < 3$). For a graphical representation of correlations between frontal SEP amplitudes and personality traits, see Figures 3 (emotion task) and 4 (gender task).

To further explore the relationship between clinical features of autism and somatosensory processing of emotional expressions, we ran the same analysis including the ASD group only. Results of the correlations confirmed the patterns observed in the whole sample of participants, showing significant correlations between individual scores on SRS-2 and AQ and SEP amplitudes specific for the emotion task. Furthermore, the analysis confirmed that Alexithymia was not significantly correlated with SEP amplitudes in any cluster and task (all ps>.25, all

494 $BF_{0-} < .80$) and interoceptive awareness was not significantly correlated with SEP amplitudes
495 (all ps >.07, all $BF_{0+} < 3$) (see Table 4 for full results).

496 In addition, we wanted to test if the individual scores on the personality questionnaires could
497 significantly predict SEP amplitudes in the frontal region, where compelling patterns of group
498 differences were observed. We ran multiple linear regressions using the backward method with
499 SRS–2, AQ, TAS-20 and MAIA-2 as predictors of SEP P100 amplitudes evoked during the
500 emotion and gender tasks. In the emotion task, the analysis yielded a highly significant model
501 ($F_{(1,30)} = 15.369$, p=.000, $R^2 = .339$, $BF_{10} = 57.092$; SEP amplitude decreased .036 μV for each
502 +1 score). The model had AQ as a single predictor. This is explained by the highly significant
503 correlations between questionnaires' scores (see Table 2A), which generated collinearity
504 between predictors. In the gender task, the same model was not significant (p=.051, BF_{10} =
505 1.553).

506 We ran the same multiple linear regression on the ASD group, and the pattern observed in the
507 whole sample was confirmed. We found a significant model for the emotion task $F_{(1,14)} = 5.210$,
508 p=.039, R^2=.271, $BF_{10} = 2.629$, SEP amplitude decreased .062 μV for each +1 score) with AQ
509 as a single predictor. Again, this is explained by the highly significant correlation between
510 questionnaires' scores in ASD (see Table 2B). We ran another linear regression with the same
511 predictors for the gender task, but also in this case the model was not significant (p=.220, BF_{10}
512 = .734).

513

514 *Source Reconstruction*

515 The best model for the TD group was the source reconstruction on 300 ms segment (log-
516 evidence -1715.8, difference with the second best model = 311.9). The winning model for the
517 ASD group was the source reconstruction on 200 ms (log evidence -1443.2, difference 6.2).

Both models showed strong evidence compared to the others because the difference in log evidence was > 50 (Ranlund et al., 2016).

P50: The main source of activity at 50 ms was localised in the right primary somatosensory cortex (S1) in both tasks for TD (coordinates: 46, -29, 54 for both tasks) and ASD (coordinates: emotion task: 42, -35, 58; gender task: 46, -31, 57).

N80: The primary source at 90 ms was located in right Brodmann Area (BA) 6 (coordinates: 12, -18, 71) for both groups and tasks. Active voxels were localised also in the right primary (S1) and secondary (S2) somatosensory cortices and in left BA6.

P100: For the TD group, the main source at 110 ms was localised in BA 6 (coordinates: 12, -18, 71 in both tasks) For the ASD group, the main source was localised in BA 6 (emotion task: 12, -18, 71; gender task: 14, -20, 69). Other active voxels were localised in the primary (S1) and secondary (S2) somatosensory cortices, right M1, left BA 6 and bilateral prefrontal areas (BA 46) for both tasks and groups. Brain maps from P100 source reconstruction of evoked activity during the emotion task can be visualised in Figure 2 D.

N140: In the TD group, for the emotion task the main source at 145 ms was localised in the right BA 6 (coordinates: 12, -18, 71), and for the gender task in BA 20 (coordinates 52, -14, -30). In the ASD group, for the emotion task the main source was localised in BA 6 (coordinates 60, -1, 22) and for the gender task in BA 20 (coordinates 52, -14, -30). Other active voxels were localised in the primary (S1) and secondary (S2) somatosensory cortices and the bilateral prefrontal cortex (BA 46) for both tasks and groups.

Visual activity (VEP) during emotion and gender visual discrimination task.

Visual activity evoked in the visual-only condition (VOC) was analysed. A summary of findings involving group differences is provided, for the full report of results (involving factors group, task, and/or emotion) and description of each analytical step, see the paragraph 'Full analysis'.

Group differences in visual processing of emotional expressions

In the P120 VEP component, the analysis revealed modulations of visual responses associated with different emotional expressions in the TD group, as shown by the significant Emotion*Electrode interaction in the right hemisphere ($F_{(2,72)}$=3.082; $p\eta^2$=.146, p=.021, however BF_{incl} = .027). In the ASD group, no interactions or main effects involving the factor emotion were found (all ps >.05, all BF_{incl} < 1/3).

In the N170 component, ASD individuals showed significantly reduced visual responses during emotion processing compared to gender, as revealed by follow-up analysis on the significant Task*Group interaction (main effect of task in ASD group: $F_{(1,18)}$ = 7.162; $p\eta^2$=.285; p=.015, BF_{10} = 3.639). No significant task-related differences were found in TD (p=.541) and no between group differences were revealed by independent-sample t-tests (all ps >.70, all BF_{incl} < 1/3).

Full analysis

P120: Results from the mixed repeated measures ANOVA showed the following significant interactions: Group*Emotion*Hemisphere*Electrode ($F_{(4,144)}$=3.613; $p\eta^2$=.091; p=.008, BF_{incl} = .027). Task*Emotion*Hemisphere ($F_{(2,72)}$ = 6.955; $p\eta^2$=.161; p=.002, BF_{incl} = .103), Task*Emotion*Electrode ($F_{(2.90,104.25)}$=3.651; $p\eta^2$=.092, p=.016, BF_{incl} = .019). To follow-up

563 the Group*Emotion*Hemisphere*Electrode interaction, we computed two separate repeated-
564 measures ANOVAs for TD and ASD groups collapsing the factor task and we found a
565 significant Emotion*Hemisphere*Electrode interaction ($F_{(4,72)}$=2.998; $p\eta^2$=.023; p=.024, BF_{incl}
566 = .019) in the TD group. No significant interactions were found in the ASD group (all ps > .05,
567 all BF_{incl} < 1/3). We computed two separate repeated-measures ANOVAs for left and right
568 hemispheres only in TD and we found a significant Emotion*Electrode interaction
569 ($F_{(2,72)}$=3.082; $p\eta^2$=.146, p=.021, BF_{incl} = .018) in the right hemisphere. We computed three
570 separate one-way ANOVAs for the three electrodes (O2, O10, PO10) but no main effects of
571 emotion were found (all ps >.05, all BF_{incl} < 1/3). No significant interactions including the
572 factor emotion were found in the left hemisphere (all ps >.05, all BF_{incl} < 1/3).

573 Moreover, we followed up the Task*Emotion*Hemisphere and Task*Emotion*Electrode
574 interactions computing two mixed repeated-measures ANOVA for the emotion and gender
575 task. Results highlighted significant Emotion*Hemisphere ($F_{(1.60,59.50)}$=5.316; $p\eta^2$=.125;
576 p=.012, BF_{incl} = .379) and Emotion*Electrode ($F_{(2.52,93.35)}$ =4.645; $p\eta^2$=.112; p=.007, BF_{incl} =
577 .019) interactions in the emotion task. We computed two repeated-measures ANOVAs
578 breaking emotion task by hemisphere and we found a significant Emotion*Electrode
579 interaction in the right hemisphere ($F_{(2.71,10.31)}$= 4.707; $p\eta^2$=.113; p=.005, BF_{incl} = .040). A
580 significant main effect of emotion was found in electrode O2 ($F_{(2,72)}$=3.841; $p\eta^2$=.094 p=.026,
581 BF_{incl} = 1.744) and Bonferroni post-hoc test revealed increased positivity for happy expression
582 compared to fearful (p=.022, BF_{10} = 18.830). No significant interactions involving the factor
583 emotion were found in the gender task (all ps > .05, all BF_{incl} < 1/3). These results suggesting
584 increased sensitivity of the right occipital visual areas during early stages of emotion
585 discrimination.

586 **N170:** We found these significant interactions involving the factor group: Task*Group ($F_{(1,36)}$
587 = 4.76; $p\eta^2$=.121; ,p=. 04, BF_{incl} = 9.093), Task*Hemisphere*Electrode*Group ($F_{(2,72)}$ = 3.988;

588 $p\eta^2$=.098, p=.04 BF_{incl} = .104). We followed-up the Task*Group interaction computing two
589 repeated-measures ANOVAs for TD and ASD groups comparing VEP amplitudes in emotion
590 and gender tasks. We found significantly decreased negativity for emotion task compared to
591 gender task in the ASD group ($F_{(1,18)}$ = 7.162; $p\eta^2$ =.285; p=.015; Bayesian paired-sample t-
592 test: BF_{10} = 3.639). No significant differences were found in the TD group (p=.541, Bayesian
593 paired-sample t-test: BF_{10} = .282). Moreover, independent-sample t-tests did not reveal
594 significant group differences (all ps>.05; Bayesian t-test: emotion task: BF_{10} = 1/3; gender task:
595 BF_{10} = .317). These results are described in Figure 5.

596 Follow-up analysis on the Task*Hemisphere*Electrode*Group (computed breaking for left
597 and right hemispheres) revealed significant Task*Group interaction in the right hemisphere,
598 electrodes PO10 of the 10/10 system ($F_{(1,36)}$ = 11.279; $p\eta^2$ =.239, p=.002, BF_{incl} = 451.38) and
599 P10 ($F_{(1,36)}$= 5.562; $p\eta^2$ =.134; p=.024, BF_{incl} = 37.465). Paired sample t-tests revealed
600 significant task differences in ASD group in electrode PO10 (t(18)=3,373, p=.003, Cohen's d
601 = .774, BF_{10} = 12.933) and P10 (t(18)=2,821, p=.011, Cohen's d = .647, BF_{0+} = 4.693) , both
602 showing increased negativity for the gender task. No differences were found in the TD group
603 and independent-sample t-tests did not show significant between-groups differences (all ps
604 >.05, all BF < 1/3).

605 Moreover, we found the following significant interaction and main effects involving the factor
606 emotion: Task*Emotion*Electrode ($F_{(3.41,123.07)}$ = 3.02; $p\eta^2$=.08; p=.02, BF_{incl} = .010),
607 Hemisphere*Emotion ($F_{(2,72)}$ = 5.75; $p\eta^2$=.14; ,p=.005, BF_{incl} = .050), Electrode*Emotion
608 ($F_{(2.90,104.62)}$ =8.48; $p\eta^2$=.19; p=.000, BF_{incl} = .012), and a main effect of emotion ($F_{(2,72)}$ = 21.90;
609 $p\eta^2$=.38; p=.000, BF_{incl} = 4552e+7).

610 To follow-up the Task*Emotion*Electrode interaction, we collapsed over groups and
611 computed two repeated-measures ANOVAs for emotion and gender tasks. Main effect of

emotion was significant in emotion task ($F_{(2,72)}$ = 14.217; $p\eta^2$=.278; p=.000, BF_{incl} = .304) and gender task ($F_{(2,72)}$ = 9.933; $p\eta^2$=.216; p=.000, BF_{incl} = 2178.310). Moreover we found a significant Electrode*Emotion interaction in the emotion ($F_{(2,72)}$ = 4.369; $p\eta^2$=.106; p=.002, BF_{incl} = 5749.421) and gender tasks ($F_{(2,72)}$ = 6.597; $p\eta^2$ =.155; p=.000, BF_{incl}=.023). A significant main effect of emotion was found in all electrode positions: Emotion Task: O1/2: $F_{(2,74)}$ = 5.395; $p\eta^2$=.127 p = .007, BF_{incl} = .281, Post-hoc (Bonferroni corrected): lower amplitude for neutral compared to fearful, p=.031, BF_{10} = 17.966 and happy, p=.010, BF_{10} = 29.232; Electrodes O9/10: $F_{(2,74)}$ = 15.052; $p\eta^2$=.289, p =.000, BF_{incl}= 4351.505), Post-hoc (Bonferroni corrected): lower amplitude for neutral compared to fearful, p=.000, BF_{10} = 138047.127 and happy, p=.000, BF_{10} = 4.786e+6; O9/10: $F_{(2,74)}$ = 15.737; $p\eta^2$=.290, p= .000, BF_{incl} = 9.986; post-hoc (Bonferroni corrected): increased negativity for fearful (p= .000, BF_{10} = 435624.724) and happy (p=.000, BF_{10} = 262931.299) compared to neutral; Gender Task: O1/2: $F_{(2,74)}$ = 3.968; $p\eta^2$=.097 p = .025, BF_{incl} = .269, Post-hoc (Bonferroni corrected): lower amplitude for neutral compared to fearful, p=.040, BF_{10} = 29.435; Electrodes O9/10: $F_{(2,74)}$ = 8.892; $p\eta^2$=.194, p =.001, BF_{incl} = 293.330), Post-hoc (Bonferroni corrected): increased negativity for fearful compared to neutral (p=.001, BF_{10} = 56614.605) and happy (p=.048, BF_{10} = 28.074); electrodesO9/10: $F_{(2,74)}$ = 13.825; $p\eta^2$=.272, p= .000, BF_{incl} = 31.280; post-hoc (Bonferroni corrected): increased negativity for fearful compared to neutral (p= .000, BF_{10} = 533077.721) and happy (p=.005, BF_{10} = 413.951).

To explore the Hemisphere*Emotion interaction, we collapsed tasks, groups and electrodes and broke the ANOVA by hemisphere. Results highlighted a main effect of emotion in the left hemisphere ($F_{(2,74)}$ = 14.431; $p\eta^2$=.281; p=.000, BF_{10} = 22.575), Post-hoc (Bonferroni corrected) revealed increased negativity for fearful compared to neutral (p=.000, BF_{10} = 2.548e+12) and happy (p=.021, BF_{10} = 295.096), and for happy compared to neutral (p=.049, BF_{10} = 283.516). Main effect of emotion was found also in the right hemisphere ($F_{(2,74)}$ =

637 23.429; $p\eta^2$ =3888 p=.000, BF_{10} = 117.131) and post-hoc (Bonferroni corrected) increased
638 negativity for fearful compared to neutral (p=.000, BF_{10} = 3.406e+14) and happy compared to
639 neutral (p=.000, BF_{10} = 1.307e+14).

640 Finally, Bonferroni corrected pairwise comparisons on the main effect of emotion revealed
641 increased negativity for fearful (p=.000, BF_{10} = 1.293e+28) and happy (p=.000, BF_{10} =
642 2.336e+15) expressions compared to neutral expressions.

643 **P250:** In this time window, we found no significant interactions or main effects involving the
644 factor group. Results exhibited significant Task*Emotion ($F_{(2,72)}$ = 4.87; $p\eta^2$ =.11, p=.01, BF_{incl}
645 = .314), and Emotion*Electrode ($F_{(4,144)}$ = 8.76; $p\eta^2$ =.19, p=.000, BF_{incl} = .009) interactions
646 and a main effect of emotion ($F_{(2,72)}$ = 3.30; $p\eta^2$ =.08, p=.04, BF_{incl} = .018). Follow-up on the
647 Task*Emotion interaction, performed breaking by task the main mixed repeated-measure
648 ANOVA, revealed a main effect of emotion in the gender task ($F_{(2,74)}$=3.921; $p\eta^2$ =.096;
649 p=.024, BF_{incl} = 1.151). Bonferroni post-hoc test did not reveal significant pairwise
650 comparisons. Nevertheless, uncorrected post-hoc test highlighted significant reduced positivity
651 for fearful compared to neutral (p=.039 BF_{10} = 27.853) and happy (p = .022, BF_{10} = 5991.424)
652 expressions. Moreover, we ran a follow-up analysis on the Emotion*Electrode interaction
653 computing three repeated-measures ANOVAs for the three electrode positions and we found a
654 main effect of emotion in electrodes PO9/10 ($F_{(2,74)}$= 7.341; $p\eta^2$=.166, p=.001, BF_{incl} = 1.924);
655 post-hoc (Bonferroni corrected) revealed a decreased positivity for fearful compared to neutral
656 (p=.003, BF_{incl} = 1285.724) and happy (p=.036, BF_{incl} = 1.505). Finally, post-hoc test
657 (Bonferroni corrected) on the main effect of emotion revealed a significantly increased positive
658 amplitude for neutral compared to fearful expressions (p=.020, BF_{10} = 2.630e+6).

659

660 *Correlations: Personality Traits and VEPs*

Correlations were computed between SRS–2, AQ, TAS-20, MAIA-2 and the VEP N170 amplitudes, where significant group and task interactions were found. We collapsed 6 electrodes over occipital areas. Results highlighted that VEP amplitudes were not significantly correlated with any of the questionnaires (all ps >.1, all BF < 1). We ran the same analysis on the ASD group only and we found a significant correlation between TAS – 20 and VEP amplitudes in emotion task (N = 19, r = -565, p=.012, BF_{10} = 5.446) and gender task (N = 19, r = -528, p=.020, BF_{10} = 3.246).

Discussion

The role of the somatosensory system in re-enacting the somatic patterns associated with the observed emotional expressions is well-established in the neurotypical population (Adolphs et al., 2000; Pitcher et al., 2008; Sel et al., 2014). Nevertheless, the hypothesis of reduced embodiment of emotional expressions in individuals with ASD is poorly investigated. In this study, we assessed the dynamics of somatosensory activity during emotion processing over and above differences in visual responses in two groups of ASD and typically developing participants. By evoking task-irrelevant SEPs, we probed the state of the somatosensory system during a visual emotion discrimination task and a control gender task. Moreover, we dissociated somatosensory from visual activity by subtracting VEPs from SEPs (Galvez-Pol et al., 2020), and compared pure somatosensory responses in ASD and TD during emotion and gender perception. We hypothesised that the two groups would differently modulate their SEPs in the emotion task but not in the gender task. Results were in line with our predictions and provided the first empirical evidence of reduced activations of the somatosensory cortex during observation and discrimination of facial emotional expressions in autistic individuals. This result is coherent with hierarchical models of face perception (Haxby et al., 2000; Calder and Young, 2005) indicating that systems beyond the visual one contribute in mapping changeable features of the observed face, such as its motion, emotion, direction of gaze, as supported by

687 studies on prosopagnosic patients or brain stimulation studies, indicating the contribution of
688 areas other than the fusiform and of the Superior Temporal Sulcus in facial emotion processing
689 (Moro et al., 2012; Candidi et al., 2015).

690 Our main finding concerns enhanced responses of the somatosensory system during emotion
691 processing in typically developed individuals compared to autistic individuals in the P100 SEP
692 component, during emotion but not gender discrimination. This pattern is consistent with TMS
693 evidence showing sequential recruitment of visual and somatosensory areas during emotion
694 processing (Pitcher et al., 2008). Group differences in somatosensory responses were
695 systematically observed in the frontal sensorimotor region, in the dorsal sites, and in the overall
696 activity. Specifically, the ASD group showed reduced P100 amplitudes compared to the TD
697 only during emotion processing, revealing reduced embodiment of emotional expressions in
698 ASD. Moreover, in the TD group, but not in ASD, we observed significantly increased P100
699 amplitudes during emotion compared to gender recognition, suggesting stronger engagement
700 of the somatosensory system during emotion compared to gender processing in the typical
701 population, but not in autistic individuals. Importantly, in the behavioural emotion and gender
702 recognition task, the ASD group showed overall decreased accuracy in catch trials compared
703 to TD; however, these behavioural differences were independent from the task. This suggests
704 that the observed task-related group differences in somatosensory responses cannot be simply
705 explained as reduced attention or poor behavioural performance during emotion discrimination
706 in ASD compared to TD.

707 Task-dependent group differences were also found in the N140 SEP component. Here, we
708 observed task-specific patterns of responses to different emotions in TD individuals which
709 were absent in ASD, suggesting persistent recruitment of the somatosensory system during
710 emotion discrimination only in the neurotypical group. This effect was localised in the right
711 hemisphere, consistently with previous literature (Adolphs et al., 2000; Pitcher et al., 2008).

712 Conversely, in the early stages of emotion processing, results suggested that the two groups
713 might be characterised by general emotion-related differences (N80).

714 Importantly, we provided further evidence on the relationship between autism and atypical
715 recruitment of the somatosensory system during emotion discrimination in mid-latency stages
716 of emotion processing. In fact, autistic traits measured by two different questionnaires (SRS-2
717 and AQ) strongly correlated with P100 amplitudes in all the clusters of electrodes where
718 significant between-group differences were observed. Importantly, only SEP amplitudes
719 evoked during the emotion task were significantly correlated with autistic traits. The
720 relationship between autistic traits and somatosensory activity during emotion processing was
721 further confirmed by the multiple linear regressions. Here we observed that the strength of
722 autistic traits, but not alexithymia, was a significant predictor of SEP amplitudes. The
723 regression model was significant only for the emotion task, and SEP amplitudes were predicted
724 both in the whole sample (considering clinical and subclinical autistic traits as a continuum,
725 see Bölte et al., 2011, Constantino & Todd, 2003, 2005; Ruzich et al., 2015) and in the ASD
726 group alone. These results highlight a persistent linear relationship between the strength of
727 autistic traits and the levels of embodiment of visually perceived emotions.

728 Crucially, alexithymia traits (measured by TAS-20) were not associated with enhanced
729 somatosensory responses, suggesting that reduced recruitment of the somatosensory system
730 during emotion discrimination is related to autism rather than alexithymia, which is often
731 associated with ASD. This result suggests that not all facets of emotion-related processing
732 difficulties observed in ASD can be attributed to co-occurring alexithymia as some have
733 suggested (Bird & Cook, 2013; Cook et al., 2013). Interestingly, interoceptive awareness was
734 correlated with emotional embodiment, which is in line with evidence implicating the insular
735 cortex in the emotion processing difficulties associated with autism (Silani et al., 2008; Ebisch
736 et al., 2011). Nevertheless, the correlation between interoceptive awareness and emotional

737 embodiment was significant only when the full cohort was considered in the analysis.
738 Conversely, no significant association between somatosensory embodiment and interoceptive
739 awareness was found when considering the ASD group only. While this discrepancy might
740 arise as a consequence of smaller sample size, it is also possible that our results reflect a general
741 association between interoception and somatosensory embodiment of emotions (and not
742 specifically related to ASD). This pattern of findings contributes to a growing literature, which
743 suggests that alexithymia and interoception may play distinct but interacting roles in the
744 emotion processing difficulties associated with ASD (e.g., Gaigg et al., 2016; Garfinkel et al.,
745 2016; Poquérusse et al., 2018; Nicholson et al., 2018).

746 Source reconstruction on the SEP components of interest revealed sources of activity in
747 primary and secondary right somatosensory cortices and right BA6. This is consistent with
748 evidence showing distributed cortical sources of SEP (Hari, et al., 1983; Harnilainen et al.,
749 1990; Allison et al., 1992; Dowman & Darcey, 1994; Allison et al., 1996; Mauguière et al.,
750 1997; Nakamura et al., 1998; Klingner et al., 2011; 2015).

751 Overall, these patterns of responses reveal a decreased engagement of the somatosensory
752 system during emotion processing in ASD compared to typical participants. These results are
753 in line with previous literature suggesting decreased vicarious representations of others' bodily
754 states in ASD (Grèzes et al., 2008; Minio-Paluello et al., 2009; Masson et al., 2019). According
755 to recent accounts, atypical top-down modulations of vicarious sensorimotor activity could be
756 implicated in reduced embodied simulation (Hamilton et al., 2013) and sensory processing
757 (Cook et al., 2012) in ASD. Therefore, it is possible that differential somatosensory responses
758 in mid-latency components in ASD and TD (P100 and N140) are driven by atypical top-down
759 modulations from high-order frontal areas. This hypothesis is in line with evidence showing
760 that SEP amplitudes, especially mid-latency components, are modulated by top-down
761 mechanisms (Josiassen et al., 1982; Michie et al., 1987; Desmedt & Tomberg, 1989; Eimer et

al., 2005; Forster & Eimer, 2005). Moreover, it is consistent with recent accounts, suggesting that somatosensory processing is implemented in a distributed neural system (de Haan & Dijkerman, 2020; Saadon-Grosman et al., 2020)

Importantly, our results cannot be explained in terms of carry-over effects from atypical visual processing in ASD. Through subtractive methods (Dell'acqua et al., 2003), we isolated somatosensory activity from visual evoked potentials and highlighted pure somatosensory responses over and above visual activity. Moreover, the analysis of VEPs did not show the same patterns of between-group differences we observed in SEPs, therefore it is unlikely that reduced embodiment is driven by cascade effects of atypical visual responses. Instead, our results suggest a specific role of the somatosensory system in triggering atypical emotion processing in ASD. In the visual N170 component, possibly arising concurrently to somatosensory processing (Pitcher et al., 2008), we observed task-related differences only in the ASD group, resulting in reduced responses during emotion recognition tasks compared to the gender task. This might underlie reduced activations of visual areas during emotion perception in ASD, as also suggested by previous studies (Kang et al., 2018; Martínez et al., 2019). Interestingly, the amplitudes of the N170 component correlated with the strength of alexithymic traits, but not autistic traits, in the ASD group, partly contradicting previous results (Desai et al., 2019) and suggesting a possible dissociation between atypical somatosensory and visual facial emotion processing related to autistic and alexithymia traits in ASD. Future research will have to systematically test this hypothesis to confirm this finding.

Our study provides novel data on atypical recruitment of the somatosensory system during emotion discrimination in ASD, suggesting reduced embodiment of the observed expressions independently from visual processing. These results offer a novel perspective on the neural dynamics underlying emotion discrimination in ASD, consistent with a theoretical framework

786 proposing that difficulties of autistic individuals in the domain of social cognition are tied to
787 reduced vicarious representations of others' bodily states.

Tables and Figures

Table 1. *Demographics and questionnaires scores for Autism Spectrum Disorder (ASD) and Typically Developing (TD) participants.*

VIQ: Verbal Intelligence Quotient; PIQ: Performance Intelligence Quotient; SRS–2: Social Responsiveness Scale; AQ: Autism Quotient; TAS-20: Toronto Alexithymia Scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness (mean ± standard deviation).

*p<.05; **p<.01

	TD	**ASD**	**Results**	**Cohen's d**	**BF_{10}**
Age	40.84 ± 12.24	40.47 ± 8.86	t(36) = .11, p=.92	.034	.316
VIQ	113.58 ± 17.80	108.56 ± 15.38	t(35) = .92, p=.37	.301	.442
PIQ	117.42 ± 13.98	111.17 ± 14.75	t(35) = 1.32, p=.194	.434	.629
SRS-2	49.29 ± 5.91	69.12 ± 11.37	t(32) = -6.39, p=.000**	2.188	30200
AQ	17.61 ± 8.79	34.89 ± 7.76	t(34) = -6.25, p=.000**	2.084	27800
TAS-20	40.42 ± 8.76	54.33 ± 14.19	t(36) = -3.63, p=.000**	1.178	34.9794
MAIA -2	3.15 ± .68	2.65 ± .81	t(36) = -3.44, p=.048*	.664	1.566

Table 2. *Correlations between questionnaires scores **A.** in the whole sample of participants and **B.** in the ASD group.*

SRS-2: Social Responsiveness Scale, Second Edition; AQ: Autism Quotient; TAS-20: Twenty-Item Toronto Alexithymia scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness, Version 2. *r*: Pearson's correlation; *p*: p-value (two-tailed); *n*: sample size; BF_{10}*:* Bayes factor.

*p<.05 (uncorrected); **p <.01 (significant after correcting for multiple correlations (Bonferroni).

A	**SRS-2**				**AQ**				**TAS-20**				**MAIA-2**			
	r	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*
SRS-2	1			34	.877	.000**	2.027e+8	32	.412	.015*	3.554	34	-.590	.000**	135.946	34
AQ					1			36	.587	.000**	184.595	36	-.542	.001**	56.029	36
TAS-20									1			38	-.214	.196	.452	38
MAIA-2													1			38
B	**SRS-2**				**AQ**				**TAS-20**				**MAIA-2**			
	r	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*	*r*	*p*	BF_{10}	*n*
SRS-2	1			17	.798	.000**	161.605	16	-.176	.500	.370	17	-.579	.015*	4.639	17
AQ					1			18	.009	.971	.292	18	-.626	.005**	1.401	18
TAS-20									1			19	-.024	.923	.285	19
MAIA-2													1			19

Figure 1. *Experimental Design.* **A.** Task: faces were presented at 500 ms from fixation cross onset and in 50% of trials tactile stimulation was delivered on the left finger after 605 ms (105 ms after face onset, following Sel et al., 2014). In 10% of trials, a question appeared after 1100 ms (Emotion Task: «Is s/he fearful?» Or «Is s/he happy?»; Gender Task: «Is s/he male?» Or «Is s/he female? ». **B.** Subtraction of Visual-Only Condition (VOC), with no tactile stimulation, from Visuo-Tactile Condition (VTC), when tactile stimulation was delivered. This method allowed us to isolate pure somatosensory evoked activity from visual carry-over effects (SEP (VEP free)). (Created with BioRender.com)

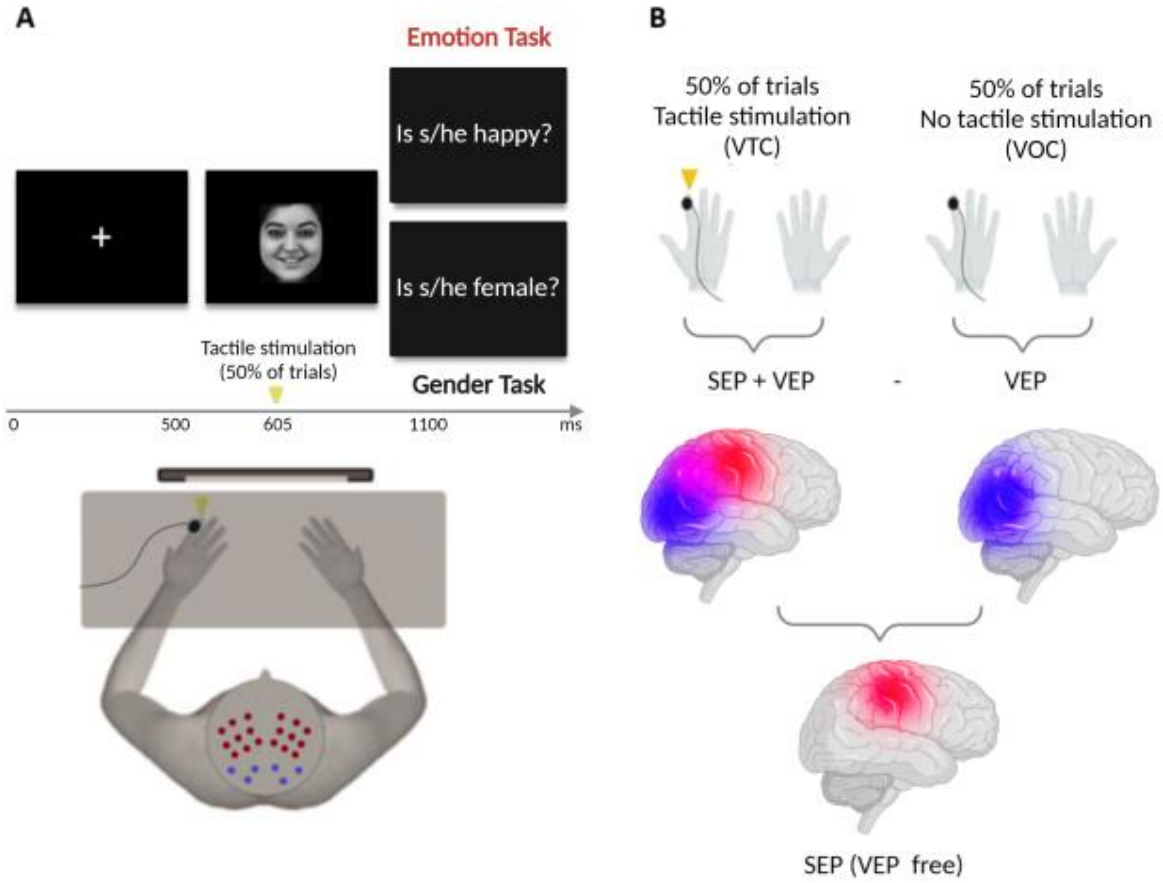


Figure 2. *SEP (VEP free) P100 results.* **A.** SEP P100 group differences in the frontal region (averaged activity of 6 electrodes), TD show enhanced positivity for emotion task compared to gender task ($p=.044$, $BF_{+0} = 3.044$) and to emotion task in ASD ($p=.047$, $BF_{+0} = 3.049$) **B.** Boxplots with individual data points of the P100 SEP amplitudes in the frontal region, in emotion and gender tasks, for the TD and ASD groups. **C.** Topographical maps of the P100 electrophysiological activity, revealing increased positivity in fronto-parietal regions during emotion processing in TD but not ASD. **D.** Source reconstruction of the P100 SEP (VEP free) component, highlights active voxels in Brodmann Area 6, Primary and Secondary somatosensory cortices, and prefrontal areas.

VOC: Visual Only Condition; VTC: Visuo-Tactile Condition; SEP: Somatosensory Evoked Potentials; VEP: Visual Evoked Potentials. (*p<.05, two-tailed).

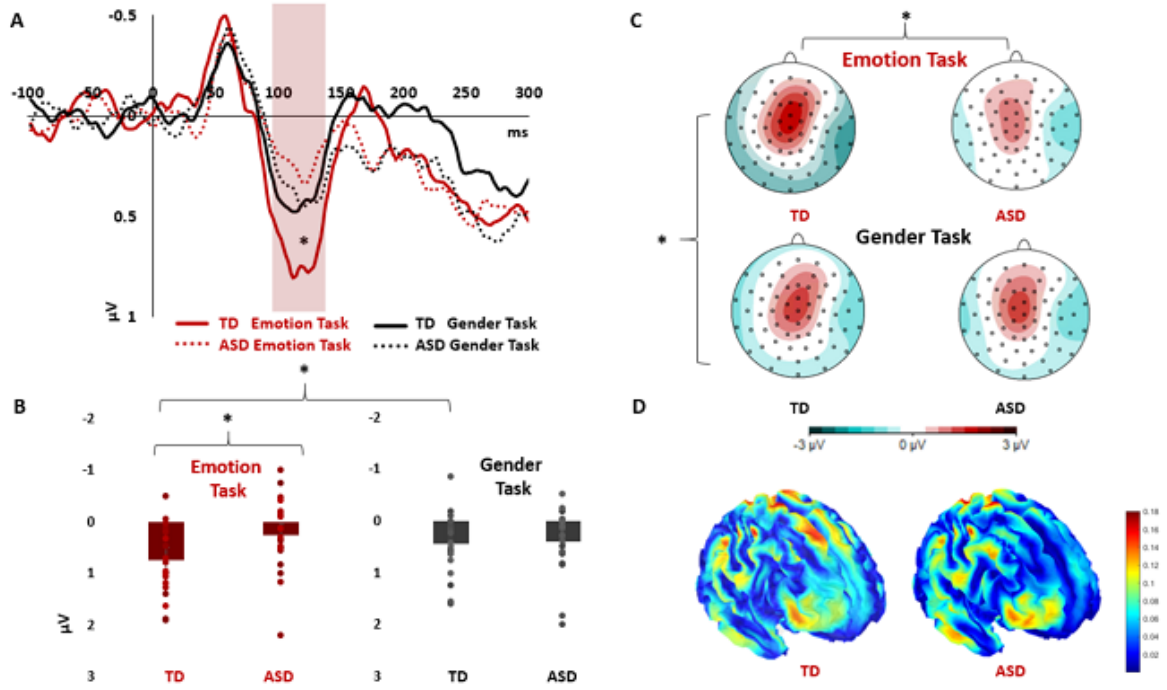


Table 3. *Correlations between autistic traits (A) alexithymia and interoceptive awareness (B) and SEP P100 amplitudes in the whole sample of participants.*

SRS–2: Social Responsiveness Scale; AQ: Autism Quotient; TAS-20: Toronto Alexithymia Scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness. Frontal emotion/gender: averaged somatosensory activity from the six electrodes placed in the frontal region; Dorsal emotion/gender: averaged somatosensory activity from the six electrodes placed in the dorsal region, close to the midline; Overall emotion/gender: averaged somatosensory activity from the eighteen electrodes placed over fronto-parietal regions. r: Pearson's correlation; p: p-value (two-tailed); BF_{0-}: Bayes Factor for negative correlation; BF_{0+}: Bayes Factor for positive correlation; n: sample size.

*p<.05 (uncorrected); **p <.01 (significant after correcting for multiple correlations (Bonferroni))

A	**SRS-2**				**AQ**			
	r	*p*	BF_{0-}	*n*	*r*	*p*	BF_{0-}	*n*
Frontal emotion	-.551	.001**	101.457	34	-.518	.001**	63.442	36
Frontal gender	-.288	.098	1.497	34	-.314	.063	2.121	36
Dorsal emotion	-.470	.005**	18.413	34	-.479	.003**	27.661	36
Dorsal gender	-.183	.299	.604	34	-.241	.157	.996	36
Overall emotion	-.539	.001**	75.863	34	-.528	.001**	79.557	36
Overall gender	-.301	.084	1.713	34	-.361	.030*	3.885	36
B	**TAS-20**				**MAIA-2**			
	r	*p*	BF_{0-}	*n*	*r*	*p*	BF_{0+}	*n*
Frontal emotion	-.276	.094	1.482	38	.417	.009**	1.539	38
Frontal gender	-.253	.126	1.164	38	.152	.361	.491	38
Dorsal emotion	-.270	.102	1.387	38	.402	.012*	8.188	38
Dorsal gender	-.241	.146	1.032	38	.095	.571	.335	38
Overall emotion	-.257	.120	1.211	38	.403	.012*	8.288	38
Overall gender	-.327	.045*	2.712	38	.153	.36	.492	38

Table 4. *Correlations between autistic traits (A) alexithymia and interoceptive awareness (B) and SEP P100 amplitudes in the ASD group.*

SRS–2: Social Responsiveness Scale; AQ: Autism Quotient; TAS-20: Toronto Alexithymia Scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness. Frontal emotion/gender: averaged somatosensory activity from the six electrodes placed in the frontal region; Dorsal emotion/gender: averaged somatosensory activity from the six electrodes placed in the dorsal region, close to the midline; Overall emotion/gender: averaged somatosensory activity from the eighteen electrodes placed over fronto-parietal regions. *r*: Pearson's correlation; *p*: p-value (two-tailed); BF_{0-}*:* Bayes Factor for negative correlation; $BF_{0+:}$ Bayes Factor for positive correlation*; n*: sample size.

*p<.05 (uncorrected); **p <.01 (significant after correcting for multiple correlations (Bonferroni)).

A	**SRS-2**				**AQ**			
	r	*p*	BF_{0-}	*n*	*r*	*p*	BF_{0-}	*n*
Frontal emotion	-.517	.034*	4.718	17	-.313	.207	1.082	18
Frontal gender	-.334	.191	1.182	17	-.155	.539	.500	18
Dorsal emotion	-.513	.035*	4.528	17	-.394	.105	1.849	18
Dorsal gender	-.240	.353	.725	17	-.238	.343	.723	18
Overall emotion	-.622	.008**	15.703	17	-.522	.026*	5.659	18
Overall gender	-.320	.211	1.093	17	-.263	.292	.823	18
B	**TAS-20**				**MAIA-2**			
	r	*p*	BF_{0-}	*n*	*r*	*p*	BF_{0+}	*n*
Frontal emotion	-.025	.919	.307	19	.214	.38	.649	19
Frontal gender	-.091	.710	.387	19	.113	.644	.420	19
Dorsal emotion	-.206	.397	.626	19	.381	.107	1.786	19
Dorsal gender	-.268	.268	.859	19	.297	.216	1.020	19
Overall emotion	-.121	.622	.433	19	.417	.076	2.354	19
Overall gender	-.241	.32	.745	19	.294	.222	.997	19

Figure 3. *Correlations between personality traits and frontal SEP P100 amplitudes in emotion task.* Autistic traits, but not Alexithymia, are significantly correlated with SEP frontal P100 amplitudes in emotion task. **A.** Social Responsiveness Scale (SRS): **p=.001, BF_{-0} = 101.457; **B.** Autism Quotient (AQ): **p=.001, BF_{-0} = 63.442; **C.** Toronto Alexithymia Scale (TAS-20): p=.094, BF_{-0} = 1.482. **D.** Interoceptive awareness measured with the Multidimensional Assessment of Interoceptive Awareness (MAIA-2) is also correlated with frontal SEP P100 amplitudes (*p=.009, BF_{+0} = 1.539).

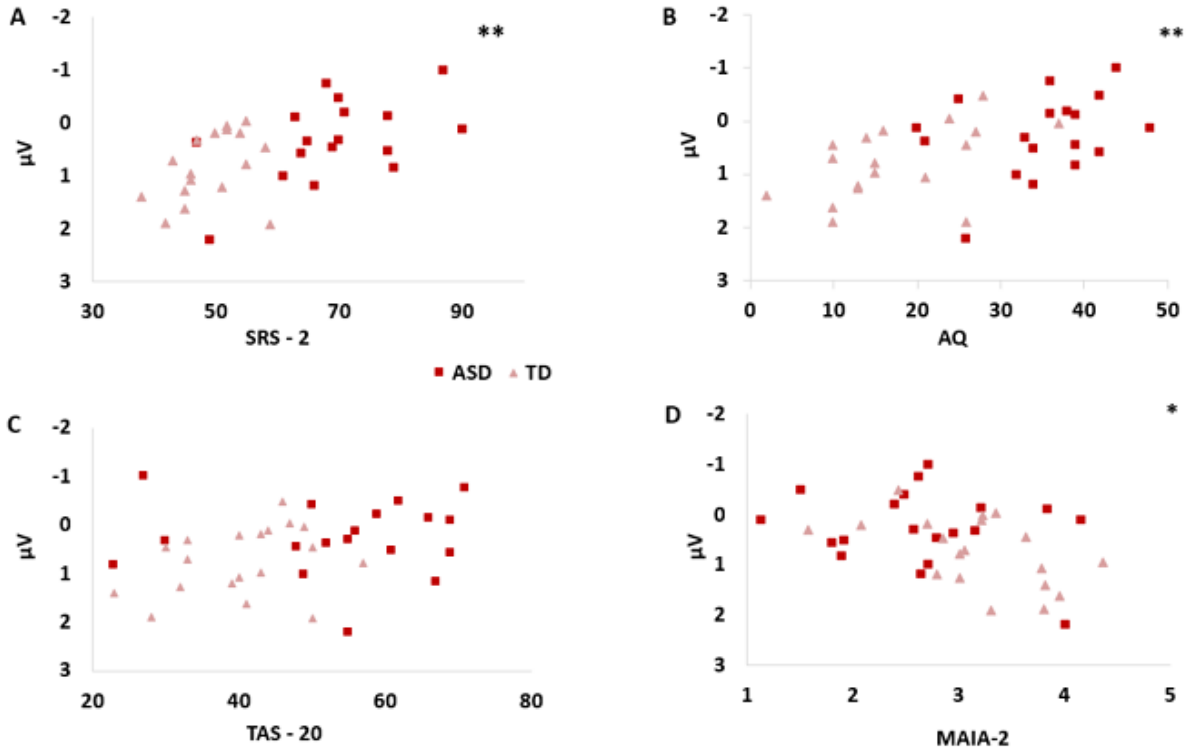


Figure 4. *Correlations between personality traits and frontal SEP P100 amplitudes in gender task.* All correlations between personality traits and frontal SEP P100 in gender task are not significant. **A.** Social Responsiveness Scale (SRS-2), p=.098, $BF_{-0} = 1.497$; **B.** Autism Quotient (AQ), p=.063, $BF_{-0} = 2.121$; **C.** Toronto Alexithymia Scale (TAS-20), p=.152, $BF_{-0} = 1.164$. **D.** Multidimensional Assessment of Interoceptive Awareness (MAIA-2), p=.361, $BF_{+0} = .491$.

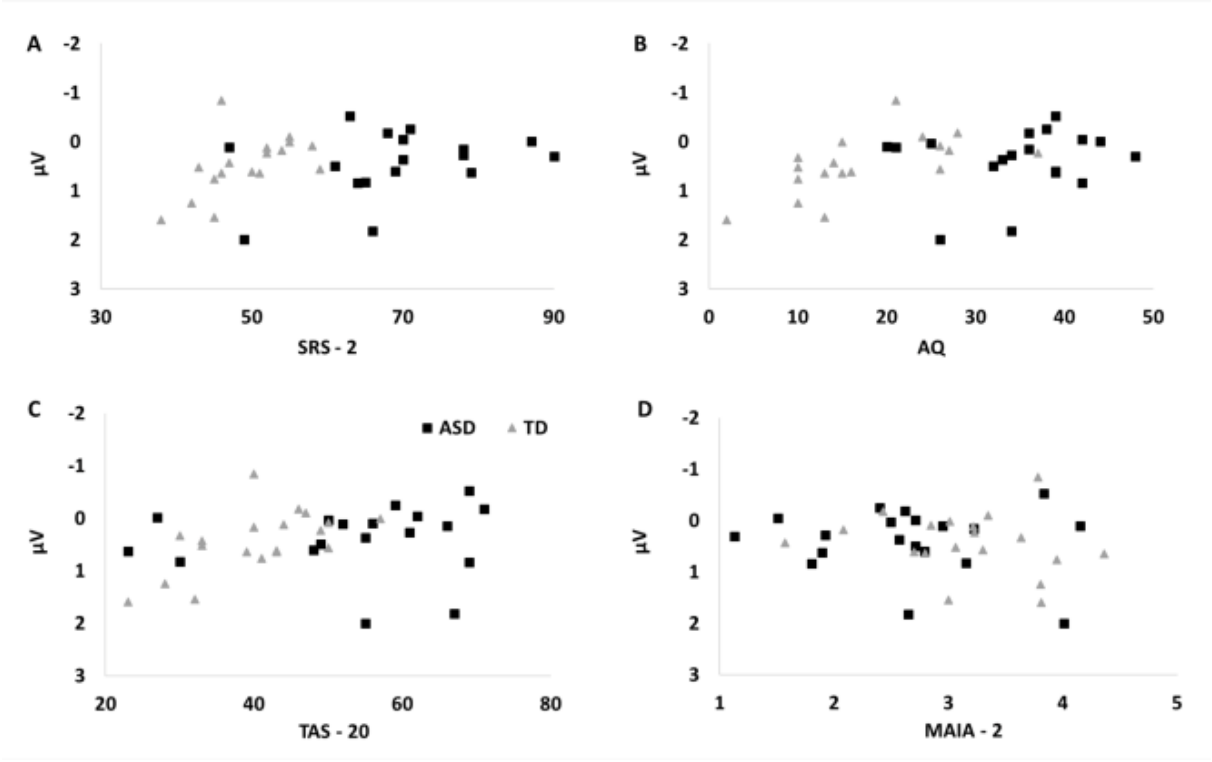
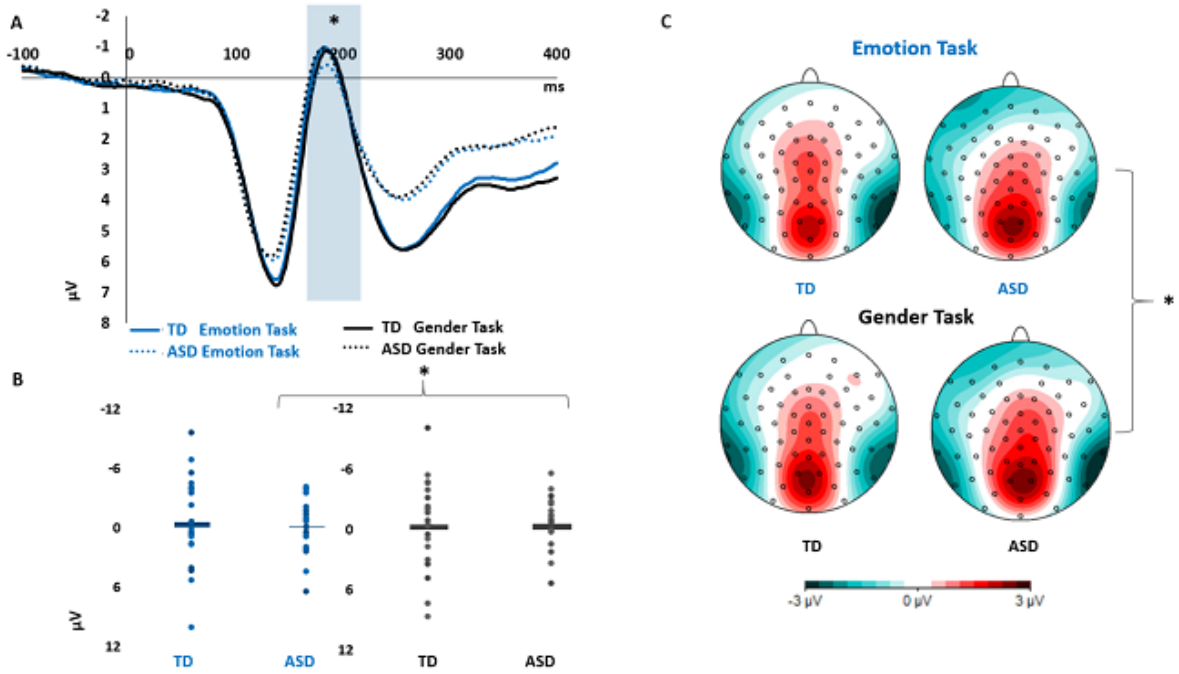


Figure 5. *VEP N170 group differences.*

A. Reduced amplitude for emotion task compared to gender task in ASD (*p=.015, BF_{10} = 3.639) but not in TD (p=.541, BF_{10} = .282). **B.** Boxplots with individual data points of the N170 VEP amplitudes in emotion and gender tasks, for the TD and ASD groups. **C**. Topographical maps of the N170 electrophysiological activity, highlighting reduced negativity over occipito-temporal regions during emotion processing compared to the control task in ASD but not TD.



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