CORTEX 167 (2023) 223–234

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research Report

Perception of facial expressions involves emotion specific somatosensory cortex activations which are shaped by alexithymia

Irena Arslanova [a,b], *Vasiliki Meletaki* [a], *Beatriz Calvo-Merino* [a] *and Bettina Forster* [a,*]

[a] *Cognitive Neuroscience Research Unit, Department of Psychology, City, University of London, UK*
[b] *Department of Psychology, Royal Holloway, University of London, UK*

ARTICLE INFO

Article history:
Received 21 March 2023
Reviewed: 3 May 2022
Revised 25 May 2023
Accepted 23 June 2023
Action Editor Sascha Frühholz
Published online 19 July 2023

Keywords:
Emotion perception
Somatosensory
ERPs
Alexithymia

ABSTRACT

Somatosensory cortex (SCx) has been shown to crucially contribute to early perceptual processes when judging other's emotional facial expressions. Here, we investigated the specificity of SCx activity to angry, happy, sad and neutral emotions and the role of personality factors. We assessed participants' alexithymia (TAS-20) and depression (BDI) levels, their cardioceptive abilities and recorded changes in neural activity in a facial emotion judgment task. During the task, we presented tactile probes to reveal neural activity in SCx which was then isolated from visual carry-over responses. We further obtain SCx emotion effects by subtracting SCx activity elicited by neutral emotion expressions from angry, happy, and sad expressions. We find preliminary evidence for distinct modulations of SCx activity to angry and happy expressions. Moreover, the SCx anger response was predicted by individual differences in trait alexithymia. Thus, emotion expressions of others may be distinctly presented in the observer's neural body representation and may be shaped by their personality trait.

1. Introduction

Judging others' emotional states is a fundamental ability that allows for smooth social interactions. The emotional state of others can be judged very efficiently from facial expressions, even without awareness (Leiberg & Anders, 2006). This rapid perception of emotional facial expressions has been linked to a distributed network of cortical and subcortical brain areas that include the visual system (e.g. occipital gyrus and fusiform gyrus), the limbic and frontal regions (amygdala, striatum and ventromedial prefrontal cortex), the insula and the right somatosensory cortex (e.g. Hussey & Safford, 2009). The importance of somatosensory cortex (SCx) in emotion processing (Kragel & LaBar, 2016; Pitcher et al., 2008; Sel et al., 2014) is supported by studies showing that damage to and

* *Corresponding author.*
E-mail address: b.forster@city.ac.uk (B. Forster).
https://doi.org/10.1016/j.cortex.2023.06.010

TMS induced disruption of right SCx disrupts emotion discrimination (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Pitcher et al., 2008). Independent contributions of SCx to emotion processing have been further confirmed by recent ERP studies (Fanghella et al., 2022; Sel et al., 2014), and are in line with theories on the embodiment of emotions (Barrett et al., 2014; Barsalou, 2009; Niedenthal, 2007).

While it has been shown that specific emotions could be mapped onto discrete brain regions, for example the amygdala for fear (Fowler et al., 2006) and the insula for disgust (Wicker et al., 2003), a more accurate view is that emotion perception is based on the interplay of neural networks that produce distributed brain states reflecting the emotional state (Lindquist et al., 2012). In line with this, Pitcher et al. (2008) showed that TMS applied to right SCx disrupted a range of different emotion perceptions. On the other hand, Kragel and LaBar's (2016) pattern analysis of right SCx BOLD activity in response to emotional facial expressions suggests, at least, emotion category specific activations of SCx (i.e. happiness and surprise versus fear and anger). Taken together, these findings indicate that right SCx is a crucial component in the processing of a range of emotions which may nevertheless be represented by, at least to some extent, distinct SCx activations. The current study aimed to clarify whether different facial emotional expressions lead to unique and reliable SCx activations in the observer and by taking advantage of the good temporal resolution of EEG and the well-defined brain basis of ERP components we expected to elucidate any differences in emotion-driven activations.

The ability to recognize emotions varies between individuals (Elfenbein & Ambady, 2002) with a wide range of factors contributing to such differences (e.g. Hodges & Wise, 2016) including personality traits (Laukka et al., 2021), affective factors (Alharbi et al., 2020; Demenescu et al., 2010) and interoceptive abilities (Georgiou et al., 2018). Alexithymia is a personality trait characterised by the inability to recognize and identify one's own and other's emotions (Bar-On & Parker, 2000; Nemiah et al., 1976). Neuroimaging studies have reported changes in the neural emotion network across a range of emotion tasks in people with high compared to low alexithymia traits (e.g. see meta-analysis by van der Velde et al., 2013) with Ihme et al. (2014) and Jongen et al. (2014) showing differences specifically in SCx and supplementary motor areas. However, while these fMRI studies show increased activity in the specific regions that allow for internally simulating others' emotions with our own body representation, it is not clear whether this activity is induced directly by the viewing of the emotional face stimuli or whether it reflects post-perceptual processes related to memorizing and appraising the emotional facial expressions. Furthermore, individual differences in emotion perception have also been linked to anxiety and depression (Demenescu et al., 2010) with the latter having been associated with alexithymia (Honkalampi et al., 2000; Li et al., 2015). In particular, high levels of depression have been shown to modulate emotion processing (Demenescu, Kortekaas, den Boer, & Aleman, 2010) and structural changes in sensory and motor systems have been implicated (Canbeyli, 2010; Ray et al., 2021). Finally, individual differences in emotion perception have also been linked to sensitivity to one's own internal, bodily states (Herbert et al., 2007; Herbert & Pollatos, 2012). In line with this notion, Georgiou et al. (2018) showed that the neural correlates of emotion perception were related to the ability to accurately perceive one's own heartbeats. Likewise, sensing and becoming aware of one's own body states, especially one's heartbeats, is subserved by a network of cortical and subcortical brain areas including somatosensory cortex (Khalsa et al., 2009). Taken together, individual differences in alexithymia, depression and cardioceptive abilities have been linked to emotion perception with some indication for changes to somatosensory activations which was investigated in the current study.

The majority of electrophysiological emotion perception studies have investigated only visual evoked responses (VEPs) (e.g. Hajcak et al., 2012 for review). VEPs elicited by the onset of emotion face stimuli do not readily reveal the induced response in somatosensory areas as VEPs amplitudes are large (3–5 μV) and spread from occipital to frontal areas. We have therefore developed a methodological approach in which we probe SCx activity with task-irrelevant touches during the processing of emotional face images (c.f. Galvez-Pol et al., 2020; Sel et al., 2014). Using this approach allowed us to reveal the induced somatosensory response and take advantage of the good temporal resolution of EEG which was recorded while participants completed a facial emotion judgment task including faces with either neutral, angry, happy, or sad expressions. We further isolated SCx emotion effects beyond any facial feature effects by subtracting neutral from emotional facial expressions (i.e. happy/angry/sad minus neutral). Based on our previous studies (Fanghella et al., 2022; Sel et al., 2014, 2020), we expected modulation of early right SCx activity (i.e. P45, N80 and P100 somatosensory components) by emotional facial expressions and confirm the presence of these early right SCx emotion effects by contrasting their amplitudes against zero activity (instead of contrasting emotion effects against each other). Furthermore, we evaluated whether any such isolated right SCx emotion effects were associated to participants' self-reported alexithymia level (Bagby et al., 1994), level of depression (Beck et al., 1996) or cardioceptive abilities (Dale & Anderson, 1978; Schandry, 1981) as these have been linked to changes in emotion perception.

2. Materials and methods

In the following sections we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants*

Thirty-five volunteers, naïve to the objective of the experiment participated for payment. The data of five participants were excluded from the EEG analyses. Two of the excluded participants had too large difference in the number of trials (after EEG cleaning) and three of them did not show clear SEP components (see EEG analysis of emotion judgment task below). The remaining 30 participants (16 women) were all

right-handed, aged 18–66 years (mean age of 27.6 years), and had normal or corrected-to-normal vision. Participants were a mix of university students, staff and people living close to the University who responded to an announcement placed on the departmental participant recruitment system (SONA). All participants who signed up during the data collection period were invited with the aim of exceeding the sample size of similar studies (Arslanova, Galvez-Pol, Calvo-Merino, & Forster, 2019; Galvez-Pol et al., 2020; Sel et al., 2014). For the cardioceptive analysis the data of one participant was excluded, because their ECG did not show clear *R* peaks (see Electrophysiological recordings below). Thus, the analyses involving cardioception were based on $N = 29$. All participants gave informed consent before participation. The study was approved by City, University of London, Psychology Research Ethics Committee.

2.2. *Facial emotion judgment task*

A set of 80 face pictures (20 per emotion) depicting angry, sad, happy, and neutral emotions from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Öhman, 1998) were grey scaled and enclosed in a rectangular frame (1.40 × 1.57 inches), excluding most of the hair and non-facial contours. Face stimuli were presented centrally on a black background using the E-prime 2 software (Psychology Software Tools, Pittsburgh, PA), which also controlled delivery of the tactile stimuli. These tactile stimuli were completely task-irrelevant, and their purpose was to probe somatosensory activity. They were delivered by 12 V solenoids (5 mm in diameter) attached with microporous tape to the tip of the left index finger. When a current passed through the solenoid tactile stimulation was delivered by driving a metal rod with a blunt conical tip that contacted participants' fingertip. To mask sounds made by the tactile stimulators, white noise (65 dB, measured from the participants' head) was presented through a loudspeaker placed 70 cm in front of the participants.

Each trial of the emotion judgement task started with the presentation of a fixation cross (500 ms), followed by a neutral, angry, sad, or happy face (600 ms). On half of the trials, in addition to a face picture, participants received brief (5 ms), task-irrelevant tactile stimulation. During the visual–tactile conditions tactile stimuli were delivered 105 ms after face onset based on previously reported right SCx emotion processing (Pitcher et al., 2008; Sel et al., 2014). To control for visual carry-over effects in the somatosensory response, we included a visual-only condition, where the same facial stimuli were presented an equal number of times as in the visual-tactile condition but without tactile stimulation (see Fig. 1A). We used 20 practice trials that did not contain any experimental facial stimuli (5 trials per condition, with 8 trials followed by a question asking about the emotion expression). The overall experiment consisted of 800 randomized trials, presented in four blocks, including 200 neutral, 200 angry, 200 sad and 200 happy faces. In 10% of all trial types of each block, participants were asked whether the face stimulus was happy, sad or angry. Participants were told to closely observe the faces presented on the screen, ignore all tactile stimuli, and to respond vocally (yes/no) as soon as possible if a question was presented (maximum response time 3000 ms). The inclusion of the question was to ensure that participants directed attention to the task and judged each facial expression. Performance was above 80% correct indicating good task compliance. Participants were offered a break in between blocks.

2.3. *Alexithymia, depression and cardioception*

To assess participants' level of alexithymia participants completed the Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994). Participants also completed the Becks Depression Inventory (Beck et al., 1996). Both questionnaires were presented before the other tasks on a computer by use of Qualtrics software (Qualtrics LLC) which also logged participants' responses.

To assess cardioceptive abilities participants completed the heartbeat counting task (Shandry, 1981). Throughout the task, presented using Eprime 2 software, a fixation cross was shown at the centre of the monitor. Participants were instructed to count their heartbeats, without feeling their pulse, when the cross turned from red to green for four randomly intermixed intervals of 20, 35, 45 and 100 s. At the end of each interval participants were asked to state the number of heartbeats they had counted and to rate their confidence in correctly counting all heartbeats on a scale of 10 with 1 signifying 'not confident at all' and 10 'very confident'. At the start of this task a 10 s practice counting interval was given. This task was performed after the questionnaires and before the emotion judgment task.

2.4. *Electrophysiological recordings*

For the EEG and ECG recordings, participants were seated in an electromagnetically shielded, sound attenuated, dimly lit room, viewing a 60 Hz computer monitor at a distance of 80 cm. EEG was recorded from 64 Ag/AgCL active electrodes of which 60 were mounted equidistantly on an elastic cap (M10 montage; EasyCap GmBH, Herrsching, Germany) and standard EEG recording preparation procedures were used to ensure good signal quality (i.e. degreasing of skin and use of electrolyte). Electrodes were referenced to the right earlobe and re-referenced off-line to the average of the scalp mounted electrodes. The horizontal electrooculogram (HEOG) was recorded by placing two electrodes about 1 cm lateral to the external canthi of each eye, and the ECG was recorded by placing one electrode about 2 cm under the left collarbone. The skin under each electrode was cleaned with an alcohol solution before conductive gel was applied. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; amplifier bandpass .01–100 Hz) and a 500 Hz sampling rate. Off-line, EEG analysis was performed using Brain Vision Analyzer 2.2 software (Brain Products GmbH, Gilching, Germany). The data was digitally low-pass-filtered at 30 Hz (Butterworth zero phase filters). The EEG signal recorded during the emotion discrimination task was epoched into segments lasting from 100 ms before to 500 ms after the onset of the tactile or visual stimuli (for analysis of somatosensory and visual activity, respectively) of each trial. Segments were then baseline corrected to the first 100 ms. Eye movements were corrected (Gratton et al., 1983) and trials with other artifacts (voltage exceeding ± 100 mV at any electrode relative to

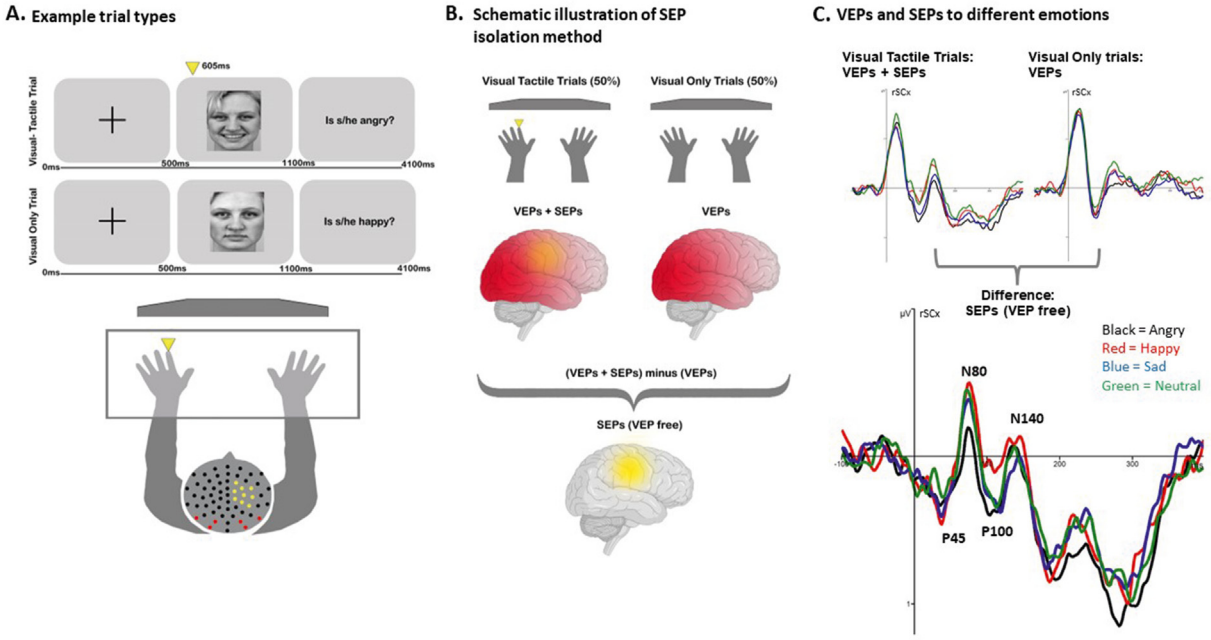

Fig. 1 – Emotion judgment task. The two different trial types of the emotion judgment task are shown and their corresponding schematic and neural responses. (A.) The left panel shows the positioning of the participants in front of the monitor including application site of the tactile probe (yellow triangle), and the distribution of recording electrodes across the scalp with yellow electrode sites included in the analyses of the SEP emotion response, and red sites in the analyses of the VEP emotion response. The timelines at the top show the sequence of visual stimuli and presentation of tactile probe in two example trial types. These trials (visual-only and visual-tactile) were randomly intermixed (50/50 ratio). A question was presented at the end of a trial in 10% of all trials. (B.) The middle panel shows the schematic neural response elicited by the onset of the images and tactile probes, and its distribution across the whole brain on an example visual-tactile (left) and visual-only (right) trial. The abstracted outcome of the subtraction of activity elicited on these two trial types is shown at the bottom. (C.) The right panel shows ERPs elicited in response to the different emotion expressions over right SCx centred on the onset of the tactile probe (at timepoint zero) on visual-tactile trials (left) and temporally equivalent on visual-only trials (right). The bottom graph shows ERPs over right SCx in response to different emotion expressions generated by subtracting ERPs on visual-only trials from visual-tactile trials resulting in VEP-free SEPs. Early somatosensory components (P45, N80, P100 and N140) are labelled and modulations of SCx activity by the different emotion expressions are shown (angry in black, happy in red, sad in blue and neutral in green).

baseline) were excluded from the analysis. For the ECG signal recorded during the heartbeat counting task the Brain Vision Analyzer 2.2 EKG detection macro was applied to identify R-peaks for each counting interval. One participant had to be excluded from this analysis as no R-peaks were detected. Heartbeat counting accuracy was then calculated based on the number of counted (HBc) and recorded (HBr) heartbeats per interval with the following formula: $1/4\sum(1-|HBr-HBc|/HBr)$. Participant's cardioceptive awareness was calculated using Pearson correlation between the counting accuracy and confidence scores (Garfinkel et al., 2015).

2.5. *EEG analysis of emotion judgment task*

To reveal the somatosensory emotion effect, we first isolated SCx activity from visual carry-over activity by subtracting brain activity on trials that contained activity only due to visual evoked responses (i.e., VEPs on visual-only trials) from trials that contained a combination of visual and somatosensory evoked responses due to the combined visual and tactile stimulus presentation (i.e., VEPs and SEPs on visual-tactile trials). This method (see Galvez-Pol et al., 2020; and Fig. 1B) allows examining somatosensory processing (SEPs) free of visually evoked activity (VEP-free). To avoid any biases, we ensured a similar level of signal-to-noise ratio between visual-tactile and visual-only trial types ($t(29) = -1.23$, $p = .23$). Two participants were excluded due to a large difference (>45 trials) in accepted trials between these two conditions. That this approach isolates somatosensory activity can be seen in Fig. 1. While somatosensory activity is not apparent in ERPs elicited on visual-only trials and only very distorted in visual-tactile trials, the subtraction of these ERPs elicited on these trial types results in difference SEPs. Importantly, common SEP components are present (i.e. P45, N80, P100 and N140) which have been shown to be generated within primary (P45) and secondary (N80 and P100) somatosensory cortex.

As a second step, we subtracted mean amplitudes of the neutral condition from mean amplitudes on each of the other emotion conditions (angry, happy, and sad) to isolate three pure emotion effects in somatosensory activity. We have

previously shown (Sel et al., 2014) that facial emotional processing modulates right somatosensory cortex (SCx) at early and mid-latency somatosensory components. This allowed us to expect specific modulations of right SCx activity, in particular in the time range of the P45, N80 and P100 components—reflecting successive stages of processing from primary (P45) to secondary (P100) SCx—for which we have previously source localized emotion modulations (Fanghella et al., 2022; Sel et al., 2014). We further pooled SEPs (VEP-free) at electrode sites corresponding to FC2, FC4, FC6, C2, C4, C6, CP2, CP4 and CP6 of the 10/10 system (electrodes 3, 4, 9, 10, 11, 12, 23, 24 and 25 of the M10 montage used in this study, respectively). These electrode sites are over right somatosensory areas where early SEP components—in particular, the P45, N80 and P100 (see Fig. 1B)—are commonly apparent and where we previously found emotion effects (Sel et al., 2014). The absence of these components (in the grand average across all emotion conditions) led to exclusion of the data of 3 participants from analysis as SCx activity was not sufficiently probed possibly due to the tactile stimulator becoming dislodged during testing. Importantly, our amplitudes subtraction approach (i.e. difference waveforms) and focus on certain ERP components and electrode sites is in line with recent ERP analysis recommendations to minimize Type I errors (Luck & Gaspelin, 2017). To confirm reliable SCx emotion effects we compared each of the right SCx emotion effects (amplitudes on angry, happy, and sad trials minus neutral trials) against zero employing planned, one-sample *t* tests and Bayes *t* tests. A comparison value of zero was used as this would indicate that the neutral and anger/happy/sad emotion expression matched. Bayes factor analysis was implemented as it allows to measure the strength of evidence for the null hypothesis (H_0)— in this case, no difference between emotion effect and zero—or the alternative hypothesis (H_a). Bayes factors with numbers smaller than 1 represent evidence for H_0 and larger than 1 for H_a (cf. Keysers et al., 2020; Teichmann et al., 2022). Analysis time windows were centred on the peaks of early and mid-latency somatosensory components (i.e. P45 (40–60 ms), N80 (66–92 ms) and P100 (94–124 ms)) where emotion effects have previously been observed (Fanghella et al., 2022; Sel et al., 2014). Analysis windows were determined by visual inspection of grand averaged SEPs (VEP-free) across all emotion conditions and participants. For the final step, to investigate the relationship between reliable SCx emotion effects and alexithymia trait, depression level and cardioceptive ability, we conducted regression analyses with mean amplitude values of the reliable SCx emotion effects as a dependent variable.

To investigate emotion effects on visual cortex (VCx), VEP grand averages were computed from the onset of the visual stimuli on visual-only trials separately for each emotion. In line with previous research (Sel et al., 2014; Williams et al., 2004; Williams, Palmer, Liddell, Song, & Gordon, 2006), we expected modulation of the P1, N170 and P2 when viewing emotional faces at electrode sites O1/2, O9/10 and PO9/10 over occipital cortex (corresponding to electrodes 44/42, 57/55 and 58/54 of the M10 layout used). Analyses windows centred on the peaks of these components (i.e., P1: 115–165 ms; N170: 167–199 ms; P2: 215–270 ms) were determined by visual inspection of the grand average across all emotions and participants. Furthermore, to investigate the pure emotion expression effects on visual processing, VEPs elicited by faces showing neutral emotion were subtracted from VEPs elicited by each of the emotion conditions (happy, sad, and angry). To confirm reliable emotion expression modulation of VEPs, one-sample *t* tests were run for each VEP emotion expression against zero based on mean amplitudes pooled over the electrodes of interest for each of the components of interest (see above). The mean amplitude of thus identified reliable VEP emotion expression effects were then submitted to regression analyses with mean amplitude values of reliable VCx emotion effects as dependent variable first and alexithymia, depression and cardioception accuracy as independent variables, mirroring the SCx emotion analysis described above. Statistical analyses were completed with SPSS (version 28) and JASP (version .16.2.0).

3. Results

3.1. Alexithymia, depression, and cardioception scores

Participants scored on average 45.62 (SD = 10.03) on the TAS-20 questionnaire with a wide spread of scores; in particular, 17 participants showed low levels of alexithymia (scoring ≤51), and 13 participants high levels of alexithymia (scoring ≥52) (Franz et al., 2008). Participants scored on average 5.6 (SD = 6.14) on the BDI, and none of the scores indicated major depression which may have influenced emotion perception. There was a strong correlation between the depression score and alexithymia (r = .61, n = 30, p = .001). Participants' heartbeat counting (cardioceptive) accuracy score was on average .62 (SD = .18), which is comparable to .66 (SD = .21) reported by Garfinkel et al. (2015). Average confidence score was 5.70 (SD = 1.62) with an average cardioceptive awareness score (i.e., the correlation coefficient between cardioceptive accuracy and confidence) of .26 (SD = .56). There was a medium correlation between cardioceptive accuracy and depression (r = .38, n = 29, p = .04) and no other significant correlations.

3.2. Analyses of SCx emotion effects, and their relation to alexithymia and cardioception

We performed planned one sample *t* tests of the emotion expression effects on right SCx activity against zero separately for the early somatosensory components (i.e. P45, N80 and P100). These showed a significant anger expression effect (M = .22. SD = .58) in the time range of the N80 component, t (29) = 2.07, p = .047, d = .38, 95% CI [.003, .439], and a happy expression effect (M = −.21, SD = .55) in the time range of the P100, t (29) = -2.13, p = .042, d = −.39, 95% CI [−.42, −.008]. There were no statistically reliable emotion expression effects in the time range of the P45 component; and there were no reliable SCx modulations of the sad emotion at any of the SEP components analysed (all t (29)<.832; p > .412; d < .142). These frequentist analysis showing insignificant effects are further supported by Bayes Factor analyses confirming an absence of evidence for any emotion effects (all BF_{10} < .3) except the N80 anger (BF_{10} = 1.3) and P100 happy (B_{10} = 1.4) emotion effects

(cf. Teichmann et al., 2022). While the evidence for the latter emotion effects is weak, it is nonetheless in favour of a difference in amplitudes of these emotion effects from zero. Fig. 1C shows SEPs (VEP-free) averaged across electrode sites over SCx in response to different emotional faces. These emotion difference waveforms indicate emotion specific modulations of SCx activity over time. Importantly, they also show the distinct somatosensory components that have been shown to be generated in primary and secondary somatosensory cortex reflecting hierarchical and distinct processing stages within somatosensory activity (Allision, 1992; Iwamura, 1998). Fig. 2 shows the isolated, mere emotion expression effects on difference waveforms of SCx activity in response to emotion faces minus neutral face expressions. These SCx emotion expression effects reveal the mere emotion effect on SCx activity with deviations from zero (indicating amplitude differences in emotion from neutral face expression) first present for anger followed by happy emotion expressions while showing only small deviations from zero over time for sad emotion expression.

Next, the relationship between the SCx embodied emotion effects with alexithymia trait score, depression and cardioceptive accuracy were analysed. As the depression level correlated with both alexithymia and cardioceptive accuracy, we conducted separate regression analyses (see Table 1). The first one looked at the effect of alexithymia while controlling

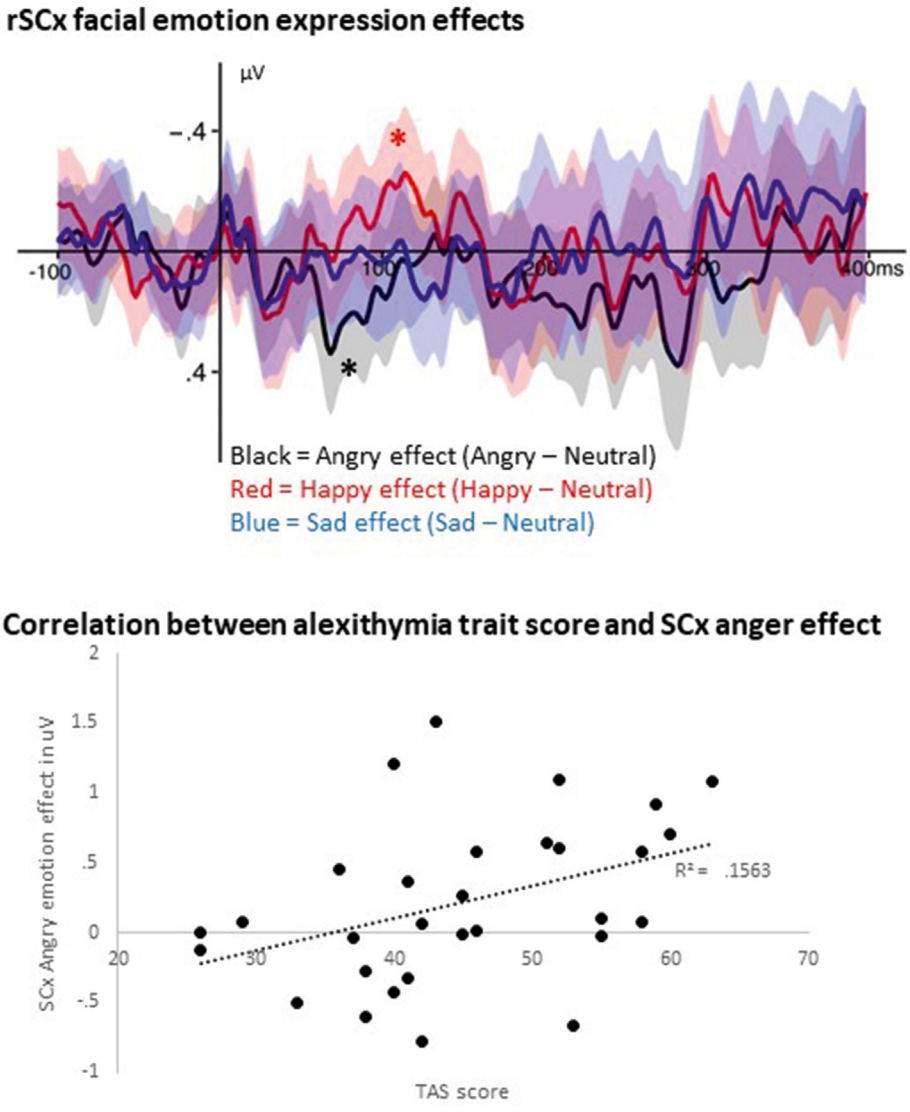

Fig. 2 – Emotion effects on somatosensory activity. Emotion effects are shown at electrodes pooled over right SCx. The top graph shows right SCx emotion effects beyond facial features over time centred on the onset of tactile probes (zero being the onset of the tactile probe), and generated by subtracting SEPs (VEP-free) elicited on neutral from angry (black line), from happy (red line) and from sad (blue line) emotion expression trials (the correspondingly shaded areas show the standard error). Asterisks indicate statistically reliable emotion effects on early somatosensory components, that is, an N80 anger and P100 happy emotion effect. The analysis time-windows were as follows: P45 (40–60 ms), N80 (66–92 ms), P100 (94–124 ms). The bottom graph shows the relationship between the rSCx anger effect and TAS score including a line representing the strength of the correlation.

Table 1 – Regression models predicting the SCx angry and happy effects.

	N80 anger effect		P100 happy effect	
	model	main predictor	model	main predictor
Alexithymia-only	**R^2=.16, P = .031**	**beta = .39(se = .17), P = .04**	R^2 = .01, p = .70	beta = −.07 (se = .19), p = .70
+ depression	**R^2=.21, P = .04**	**beta = .57(se = .22), P = .01**	R^2 = .01, p = .93	beta = −.08 (se = .24), p = .74
+ cardioception	R^2 = .18, p = .17	beta = .51 (se = .24), p = .05	R^2 = .07, p = .58	beta = −.23 (se = .26), p = .37
Cardioception-only	R^2 = .02, p = .45	beta = −.15 (se = .19), p = .45	R^2 = .04, p = .29	beta = −.20 (se = .18), p = .29
+ depression	R^2 = .04, p = .63	beta = −.20 (se = .21), p = .36	R^2 = .04, p = .56	beta = −.22 (se = .21), p = .30
+ alexithymia	R^2 = .18, p = .17	beta = −.06 (se = .21), p = .78	R^2 = .07, p = .58	beta = −.28 (se = .22), p = .21

Note: main predictor column shows the beta values for the main predictor in bold, alexithymia and cardioception, respectively.

for depression and cardioceptive accuracy and the second one looked at the effect of cardioceptive accuracy while controlling for depression and alexithymia. One participant was missing a cardioception score, resulting in an exclusion (see Participants section above). All variables were standardised and mean-centred. Table 1 shows that only modelling the effect of alexithymia on the N80 anger component was statistically significant. Higher levels of alexithymia predicted stronger SCx activation in response to angry as opposed to neutral expressions in the N80 time window (see Fig. 2 lower panel; without controlling depression or cardioception: $t = 2.3$, $p = .04$). The effect of alexithymia was strengthened when controlling for depression ($t = 2.6$, $p = .01$) and marginally retained when cardioception was included into the model ($t = 2.1$, $p = .05$). Alexithymia did not predict the P100 happy effect and cardioceptive accuracy did not predict SCx modulations for either emotion.

3.3. *Analyses of VCx emotion effects, and its relation to alexithymia and cardioception*

Planned one sample t-tests of the visual emotion expression effects against zero showed a significant anger expression effect on VCx activity ($M = -.72$, SD = 1.14) in the time range of the P2, t (29) = −3.46, $p = .002$, $d = -.63$, 95% CI [−1.15, .29]. There were no statistically reliable happy or sad emotion expression effects (happy: all t (29) > .09, $p > -1.78$, $d < -.33$; sad: all t (29) > −1.58, $p > .13$, $d < -.29$) in the time range of the P1 or N170 components; and there were no reliable VCx modulations of sad expressions at any of the VEP components analysed (all t (30) < −1.315; $p > .199$). Importantly, the anger expression effect on SCx was seen on the somatosensory N80 component. The analysis time window for this component (66 ms–92 ms after tactile probe onset and 171 ms to 197 ms from the visual stimulus onset) precedes the analysis window for the visual P2 component (215 ms–270 ms after visual onset and 110–165 ms after tactile onset). In addition, anger effect amplitudes did not correlate ($r = .08$, $p = .68$), further confirming the independence of the SCx anger expression effect from the anger VEP emotion effects. Furthermore, none of the regression models with the visual P2 anger expression effect as a dependent variable and alexithymia, depression, and cardioceptive accuracy as independent variables were significant (see Table 2). The top graph of Fig. 3 shows VEPs averaged across electrode sites over VCx in response to different emotional faces revealing emotion specific modulations of VCx activity over time, while the bottom graph shows the visual emotion expression effects, that is difference waveforms of VCx activity in response to emotion faces minus neutral face expressions. These emotion expression effects on VCx activity reveal the pure emotion effect on VCx activity with deviations from zero present for angry, but comparatively small for happy and sad face expressions.

4. Discussion

A neural network of brain areas subserves the rapid understanding of other's emotion expressions allowing for smooth social interactions. The right SCx has been shown to independently contribute to the early visual perceptual processing underpinning such social interactions (Pitcher et al., 2008; Sel et al., 2014). This has contributed to the view of emotional understanding as not merely conceptual but as an embodied phenomenon engaging one's own internal body representation (Barrett et al., 2014; Barsalou, 2009; Niedenthal, 2007). The current study expands those previous findings by showing preliminary evidence that SCx engagement during perception of emotional facial expressions is emotion-specific and shaped by trait alexithymia. This suggests that perceiving emotions in others may engage the internal body representation to varying degrees as a function of one's own emotional abilities. Specifically, we recorded ERPs in response to neutral, happy, angry, and sad faces and isolated the neural response to the emotional face images over somatosensory areas. To reveal the SCx response during the facial emotion judgment task, we probed SCx activity by task-irrelevant touches (visual-tactile trials) and subtracted VEPs elicited on visual-only trials to generate VEP-free SEPs. We isolated emotion effects by subtracting SEP amplitudes (VEP-free) on trials with emotional facial expressions from trials with neutral expressions and proceeded to show distinct modulations of somatosensory activity for anger in the time range of the somatosensory N80 followed by a happy emotion effect for the P100 component. Furthermore, the magnitude of the earlier somatosensory modulation by anger was further shaped by self-reported alexithymia.

In previous studies (Fanghella et al., 2022; Sel et al., 2014) we have shown right SCx emotion modulations at early and mid-latency time ranges. While these studies showed that SCx activity is enhanced when judging emotions compared to the person's gender, they also showed differential engagement of SCx to different emotions (e.g. fearful differs from happy). Here we show that the isolated SCx emotion effect induced

Table 2 – Regression models predicting the VCx angry effect.

	P2 anger effect	
	model	main predictor
Alexithymia-only	$R^2 < .001.$, $p = .93$	beta = .02 (se = .19), $p = .93$
+ depression	$R^2 = .02$, $p = .80$	beta = −.08 (se = .24), $p = .74$
+ cardioception	$R^2 = .04$, $p = .77$	beta = −.20 (se = .26), $p = .45$
Cardioception-only	$R^2 = .003$, $p = .80$	beta = −.05 (se = .19), $p = .80$
+ depression	$R^2 = .02$, $p = .80$	beta = −.11 (se = .21), $p = .62$
+ alexithymia	$R^2 = .04$, $p = .77$	beta = −.16 (se = .22), $p = .45$

Note: main predictor column shows the beta values for the main predictor in bold, alexithymia and cardioception, respectively.

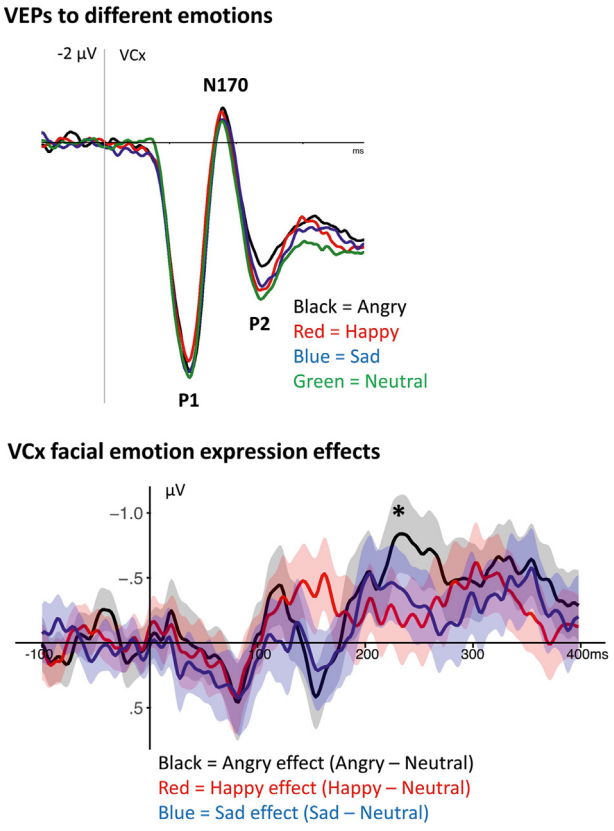

Fig. 3 – Emotion effects on visual activity. Emotion effects re shown at electrodes pooled over VCx. The top graph shows VEPs elicited in response to different emotion images (zero being the onset of the images) with different line colours representing different emotional facial expressions. The bottom graph of difference ERPs showing the emotion effect in VCx activity. These waveforms were generated by subtracting VEPs elicited by neutral from angry (black line), from happy (red line) and from sad (blue line) facial expressions on visual-only emotion expression trials (the correspondingly shaded areas show the standard error). Asterisk indicates the statistically reliable anger emotion effect in the time range of the P2 visual component. The analysis time-windows were as follows: P1 (115–165 ms), N170 (167–195 ms), P2 (215–270 ms).

when discriminating other's angry and happy emotional facial expressions exceeds neutral emotion expressions effects. Furthermore, right SCx anger preceded happy activations suggesting unique temporal pattern of activations possibly linked to different somatosensory processing stages (N80 versus P100). Employing repetitive TMS, Pitcher et al. (2008) established a functional role of SCx in perception of facial expressions conveying happy, sad, surprise, fear, disgust, and anger. However, they were not able to show expression-specific effects possibly due to the restricted number of trials employed per emotion (see Pitcher et al., 2008 for discussion). We demonstrate temporally distinct SCx emotion effects for perceiving angry and happy facial expressions.

One tentative explanation for the emotion specific SCx activations is that different emotions vary in the level and the nature of the somatovisceral representation they involve (Hussey & Safford, 2009). A series of studies using event-related desynchronisation (ERD) have similarly shown a distinct profile of neural rhythms within the sensorimotor and SCx regions, in particular between expressions of happiness and disgust (Moore et al., 2012) and between happiness and fear and sadness (Charidza & Gillmeister, 2022). Charidza and Gillmeister (2022) interpret the increased ERD when viewing happy versus sad and fearful expressions as arising from a potential greater simulation of positive motor action inherent in a happy expression or due to perceptual advantage of happy expressions, whereby happy expressions are easier to decode than those of sadness (Kirita & Endo, 1995). Likewise, in the present study, significant modulations of SCx-related activity when viewing happy and angry expressions, but not sad expressions, relative to neutral expressions, may be because expressions of happiness and anger recruit greater somatovisceral representations as opposed to expressions of sadness. While it is possible that SCx sad emotion effect takes longer to develop and that the timing with which we probed somatosensory activations with regards to the onset of the visual facial stimuli may have not been optimal for sad emotion expressions, Charidza and Gillmeister (2022) used dynamic emotional expressions lasting 4 s.

The reason for a distinct early SCx response for angry (N80) and a slightly later response for happy (P100) expressions remains unclear. There are several reasons why somatovisceral response to expressions of anger and happiness should differ. First, that the anger effect precedes the happy SCx effect may reflect the evolutionary significance of anger perception or that anger typically involves a more rapid engagement of somatovisceral processes (i.e., quick acceleration of the heart). Second, while expression of happiness may engage stronger internal simulation to augment the positive affective state (Soussignan, 2002), expression of anger may involve less

simulation as it is a non-affiliative signal (Bourgeois & Hess, 2008). Interestingly, an early differentiation (around 80 ms) between neutral and angry expression over SCx was followed by a later anger differentiation (around 200 ms) over the occipital areas. P200 is known to be the first component that shows emotion specificity, for example it is enhanced for fearful as compared to happy and neutral faces (Eimer & Holmes, 2002; Ashley et al., 2004). It could be that the rapid engagement of somatovisceral processes during the perception of anger translated to better emotion detection as reflected in the P200 modulation over the VCx. However, it should be noted that both happy and anger emotion effects were driven by a decrease in the respective components relative to the neutral emotion. However, the meaning of this directionality and the functional significance of temporally distinct emotion specific SCx modulation remain unclear. It should also be noted that the SCx modulations when viewing angry and happy expressions as opposed to neutral ones remained statistically marginal. Thus, further studies with a more stringent emotion task would be required to tie ERP modulations to behavioural outcomes.

In addition, we investigated the role of trait alexithymia, depression levels and cardioceptive abilities in shaping this neural emotion response right SCx when observing other's facial expressions. Neurological and psychiatric disorders such as Schizophrenia have been linked to reduced and slower ERP components during perception of faces (Feuerriegel et al., 2015) and reduced differentiations between happy, sad and happy, fearful expressions have been found over SCx in individuals with higher trait anxiety and trait autism, respectively (Charidza & Gillmeister, 2022). Here we show that individual differences in the levels of alexithymia predict, in part, the outcome of the SCx N80 anger emotion effect and this relationship was even strengthened when considering depression levels. Deficits in social interactions and emotion recognition are a key feature in people who have high levels of trait alexithymia (Nemiah et al., 1976). Interestingly, levels of alexithymia were related to a greater difference in SCx activity between the expression of anger and neutral expression. Yet, this finding extends the findings of a previous fMRI study (Ihme et al., 2014) in which a higher BOLD response in SCx in response to angry and fearful expressions, but not happy expressions was reported in the high compared to low alexithymia group, suggesting an enhanced somatosensory processing when faced with angry and fearful expressions. Ihme et al. (2014) interpreted the enhanced somatosensory processing in high alexithymia as reflecting the possibility that alexithymic individuals may rely more strongly on information related to bodily actions or may be more inclined to internally simulate the expressions of others. The lack of correlation between trait alexithymia and SCx happy effect is also consistent with the findings of Ihme et al. (2014) and may be related to fewer difficulties of interpreting the positive expressions (Sonnby-Borgström et al., 2009) or it could be related to the fact that expression of anger is more salient signal for survival than the expression of happiness and thus needs to be processed to a greater extent. To elucidate the functional significance of the greater SCx response when perceiving anger with higher levels of alexithymia future studies may examining accuracy scores in a more demanding emotion judgement task (i.e., with morphed neutral-to-emotional expressions).

Finally, we also evaluated participants cardioceptive abilities, in the form of the commonly used heartbeat counting task (Dale & Anderson, 1978; Schandry, 1981), as many theories of emotion processing have postulated a close relationship with the perception of physiological signals (e.g. Damasio, 1999; James, 1884; Schachter & Singer, 1962). Likewise, previous research has shown links between heartbeat counting accuracy and empathy for others (Grynberg & Pollatos, 2015), neural markers of emotional self-regulation (Füstös et al., 2013; Herbert et al., 2007) and understanding the emotional expressions of others (Georgiou et al., 2018; Herbert et al., 2007; Herbert & Pollatos, 2012). Yet, we did not find that the heartbeat counting accuracy predicted neural measures of VCx or SCx emotion effects. However, it should be noted, that the ability to accurately count one's heartbeat may be influenced by prior knowledge of the timing of one's heartbeat (Brener & Ring, 2016) or exteroceptive information (Khalsa et al., 2009) and control measures have been suggested (Murphy et al., 2018).

Taken together, we show differences in the right SCx emotion effect to observed anger and happy facial expressions extending previous findings showing an independent role of SCx in emotion processing (Pitcher et al., 2008; Sel et al., 2014). Moreover, we show that individual differences in the personality trait alexithymia account, at least in part, for the SCx anger emotion effect. Therefore, the neural response when observing other's emotions in SCx can be unique to the observed emotion and, at least for anger, can be shaped by the observer's alexithymia trait.

Open practices section

The study in this article earned Open Data and Open Material badges for transparent practices. The data and the study material underlying this article have been made available on this OSF project page: https://osf.io/3bg2a/?view_only=fc7db428a02d4e47beac3bf1c5eac8a8 and this Figshare folder: https://doi.org/10.25383/city.21303342.v2.

Data and study material availability

The data and the study material underlying this article have been made available on this OSF project page: https://osf.io/3bg2a/?view_only=fc7db428a02d4e47beac3bf1c5eac8a8 and this Figshare folder: https://doi.org/10.25383/city.21303342.v2. No part of the study procedures or analysis plans was preregistered prior to the research being conducted. For further questions and requests in respect to the study data or material, please contact the corresponding author.

Funding

This research was supported by a undergraduate research bursery by the Experimental Psychology Society (EPS) to I.A. and B.F.

Author statement

Irena Arslanova: Conceptualization, Methodology, Software, Investigation, Formal Analysis, Writing–Review & Editing, Funding Acquisition. Vasiliki Meletaki: Formal Analysis; Writing–Review & Editing. Beatriz Calvo-Merino: Conceptualization; Writing–Review & Editing. Bettina Förster: Conceptualization, Methodology, Software, Formal Analysis, Writing–Original Draft & Review & Editing, Supervision, Funding Acquisition.

REFERENCES

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, A. R. (2000). A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J Neurosci, 20*, 2683–2690.

Alharbi, S., Button, K., Zhang, L., O'Shea, K. J., Fasolt, V., Lee, A. J., DeBruine, L. M., & Jones, B. C. (2020). Are affective factors related to individual differences in facial expression recognition? *Royal Society open science, 7*(9), Article 190699. https://doi.org/10.1098/rsos.190699

Allison, T., McCarthy, G., & Wood, C. C. (1992). The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalography and Clinical Neurophysiology, 84*(4), 301–314. https://doi.org/10.1016/0168-5597(92)90082-m

Arslanova, I., Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2019). Searching for bodies: ERP evidence for independent somatosensory processing during visual search for body-related information. *NeuroImage, 195*, 140–149. https://doi.org/10.1016/j.neuroimage.2019.03.037.

Ashley, V., Vuilleumier, P., & Swick, D. (2004). Time course and specificity of event-related potentials to emotional expressions. *Neuroreport, 15*(1), 211–216.

Bagby, R. M., Parker, J. D., & Taylor, G. J. (1994). The twenty-item Toronto Alexithymia Scale–I. Item selection and cross-validation of the factor structure. *Journal of Psychosomatic Research, 38*(1), 23–32. https://doi.org/10.1016/0022-3999(94)90005-1

Bar-On, R., & Parker, J. D. A. (2000). *The handbook of emotional intelligence: Theory, development, assessment, and application at home, school, and in the workplace*. San Francisco, California: Jossey-Bass.

Barrett, L. F., Wilson-Mendenhall, C. D., & Barsalou, L. W. (2014). A psychological construction account of emotion regulation and dysregulation: The role of situated conceptualizations. In J. J. Gross (Ed.), *Handbook of emotion regulation* (pp. 447–465). New York, NY: Guilford.

Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philos. Trans. R. Soc. Lond. B Biol. Sci., 364*, 1281–1289. https://doi:10.1098/rstb.2008.0319.

Beck, A. T., Steer, R. A., & Brown, G. K. (1996). *Manual for the Beck depression inventory-II*. San Antonio, TX: Psychological Corporation.

Bourgeois, P., & Hess, U. (2008). The impact of social context on mimicry. *Biological psychology, 77*(3), 343–352.

Brener, J., & Ring, C. (2016). Towards a psychophysics of interoceptive processes: The measurement of heartbeat detection. *Phil. Trans. R. Soc. B, 371*(1708), Article 20160015. https://doi.org/10.1098/rstb.2016.0015

Canbeyli, R. (2010). Sensorimotor modulation of mood and depression: An integrative review. *Behavioural Brain Research, 207*(2), 249–264. https://doi.org/10.1016/j.bbr.2009.11.002

Charidza, C. A., & Gillmeister, H. (2022). Differential beta desynchronisation responses to dynamic emotional facial expressions are attenuated in higher trait anxiety and autism. *Cognitive, Affective & Behavioral Neuroscience, 22*(6), 1404–1420.

Dale, A., & Anderson, D. (1978). Information variables in voluntary control and classical conditioning of heart rate: Field dependence and heart-rate perception. *Perceptual and Motor Skills, 47*(1), 79–85. https://doi.org/10.2466/pms.1978.47.1.79

Damasio, A. R. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. New York: Harcourt Brace.

Demenescu, L. R., Kortekaas, R., den Boer, J. A., & Aleman, A. (2010). Impaired attribution of emotion to facial expressions in anxiety and major depression. *Plos One, 5*(12), Article e15058. https://doi.org/10.1371/journal.pone.0015058

Demenescu, L. R., Kortekaas, R., den Boer, & Aleman, A. (2010). Impaired attribution of emotion to facial expressions in anxiety and major depression. *PloS one, 5*(12), Article e15058. https://doi.org/10.1371/journal.pone.0015058.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport, 13*(4), 427–431.

Elfenbein, H. A., & Ambady, N. (2002). On the universality and cultural specificity of emotion recognition: A meta-analysis. *Psychological Bulletin, 128*, 203–235. https://doi.org/10.1037/0033-2909.128.2.203

Fanghella, M., Gaigg, S. B., Candidi, M., Forster, B., & Calvo-Merino, B. (2022). Somatosensory evoked potentials reveal reduced embodiment of emotions in autism. *The Journal of Neuroscience, 42*(11), 2298–2312. https://doi.org/10.1523/JNEUROSCI.0706-21.2022

Feuerriegel, D., Churches, O., Hofmann, J., & Keage, H. A. (2015). The N170 and face perception in psychiatric and neurological disorders: A systematic review. *Clinical Neurophysiology, 126*(6), 1141–1158.

Fowler, H. L., Baker, G. A., Tipples, J., Hare, D. J., Keller, S., Chadwick, D. W., & Young, A. W. (2006). Recognition of emotion with temporal lobe epilepsy and asymmetrical amygdala damage. *Epilepsy & Behavior, 9*(1), 164–172. https://doi.org/10.1016/j.yebeh.2006.04.013

Franz, M., Popp, K., Schaefer, R., Sitte, W., Schneider, C., Hardt, J., Decker, O., & Braehler, E. (2008). Alexithymia in the German general population. *Social Psychiatry and Psychiatric Epidemiology, 43*(1), 54–62. https://doi.org/10.1007/s00127-007-0265-1

Füstös, J., Gramann, K., Herbert, B. M., & Pollatos, O. (2013). On the embodiment of emotion regulation: Interoceptive awareness facilitates reappraisal. *[Social Cognitive and Affective Neuroscience Electronic Resource], 8*(8), 911–917. https://doi:10.1093/scan/nss089.

Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2020). Revealing the body in the brain: An ERP method to examine sensorimotor activity during visual perception of body-related information. *Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 125*, 332–344. https://doi.org/10.1016/j.cortex.2020.01.017

Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. *Biological psychology, 104*, 65–74.

Georgiou, E., Mai, S., Fernandez, K. C., & Pollatos, O. (2018). I see neither your Fear, nor your Sadness - interoception in adolescents. *Consciousness and Cognition, 60*, 52–61. https://doi.org/10.1016/j.concog.2018.02.011

Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology, 55*, 468–484.

Grynberg, D., & Pollatos, O. (2015). Perceiving one's body shapes empathy. *Physiology & Behavior, 140*, 54–60. https://doi.org/10.1016/j.physbeh.2014.12.026

Hajcak, G., Weinberg, A., MacNamara, A., & Foti, D. (2012). ERPs and the study of emotion. In E. S. Kappenman, & S. J. Luck (Eds.), *Oxford handbook of ERP components* (pp. 441–474). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780195374148.013.0222.

Herbert, B. M., & Pollatos, O. (2012). The body in the mind: On the relationship between interoception and embodiment. *Topics in Cognitive Science, 4*(4), 692–704.

Herbert, B. M., Pollatos, O., & Schandry, R. (2007). Interoceptive sensitivity and emotion processing: An EEG study. *Int J Psychophysiol, 65*(3), 214–227.

Hodges, S. D., & Wise, A. A. P. (2016). Interpersonal accuracy: Real and perceived links to prosocial behavior. In J. A. Hall, M. S. Mast, & T. V. West (Eds.), *The social psychology of perceiving others accurately* (pp. 350–375). Cambridge University Press.

Honkalampi, K., Hintikka, J., Tanskanen, A., Lehtonen, J., & Viinamäki, H. (2000). Depression is strongly associated with alexithymia in the general population. *Journal of Psychosomatic Research, 48*, 99–104.

Hussey, E., & Safford, A. (2009). Perception of facial expression in somatosensory cortex supports simulationist models. *The Journal of Neuroscience, 29*(2), 301–302. https://doi.org/10.1523/JNEUROSCI.5205-08.2009

Ihme, K., Sacher, J., Lichev, V., Rosenberg, N., Kugel, H., Rufer, M., Grabe, H.-J., Pampel, A., Lepsien, J., Kersting, A., Villringer, A., & Suslow, T. (2014). Alexithymia and the labeling of facial emotions: Response slowing and increased motor and somatosensory processing. *BMC Neuroscience, 15*, 40. https://doi.org/10.1186/1471-2202-15-40

Iwamura. (1998). Hierarchical somatosensory processing. *Current Opinion in Neurobiology, 8*(4), 522–528. https://doi.org/10.1016/S0959-4388(98)80041-X

James, W. (1884). What is an emotion? *Mind, 9*, 188–205.

Jongen, S., Axmacher, N., Kremers, N. A. W., Hoffmann, H., Limbrecht-Ecklundt, K., Traue, H. C., & Kessler, H. (2014). An investigation of facial emotion recognition impairments in alexithymia and its neural correlates. *Behavioural Brain Research, 271*, 129–139. https://doi.org/10.1016/j.bbr.2014.05.069

Keysers, C., Gazzola, V., & Wagenmakers, E. J. (2020). Using Bayes factor hypothesis testing in neuroscience to establish evidence of absence. *Nature Neuroscience, 23*, 788–799. https://doi.org/10.1038/s41593-020-0660-4

Khalsa, S. S., Rudrauf, D., Feinstein, J. S., & Tranel, D. (2009a). The pathways of interoceptive awareness. *Nature Neuroscience, 12*(12), 1494–1496. https://doi.org/10.1038/nn.2411

Khalsa, S. S., Rudrauf, D., Sandesara, C., Olshansky, B., & Tranel, D. (2009b). Bolus isoproterenol infusions provide a reliable method for assessing interoceptive awareness. *International Journal of Psychophysiology, 72*(1), 34–45. https://doi.org/10.1016/j.ijpsycho.2008.08.010

Kirita, T., & Endo, M. (1995). Happy face advantage in recognizing facial expressions. *Acta psychologica, 89*(2), 149–163.

Kragel, P. A., & LaBar, K. S. (2016). Somatosensory representations link the perception of emotional expressions and sensory experience. *eNeuro, 3*(2), 90. https://doi.org/10.1523/ENEURO.0090-15.2016, 15.2016.

Laukka, P., Bänziger, T., Israelsson, A., Cortes, D. S., Tornberg, C., Scherer, K. R., & Fischer, H. (2021). Investigating individual differences in emotion recognition ability using the ERAM test. *Acta Psychologica, 220*, Article 103422. https://doi.org/10.1016/j.actpsy.2021.103422

Leiberg, S., & Anders, S. (2006). The multiple facets of empathy: A survey of theory and evidence. *Progress in Brain Research, 156*, 419–440. https://doi.org/10.1016/S0079-6123(06)56023-6

Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: A meta-analytic review. *The Behavioral and Brain Sciences, 35*(3), 121–143. https://doi.org/10.1017/S0140525X11000446

Li, S., Zhang, B., Guo, Y., & Zhang, J. (2015). The association between alexithymia as assessed by the 20-item Toronto alexithymia scale and depression: A meta-analysis. *Psychiatry Research, 227*, 1–9.

Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology, 54*(1), 146–157. https://doi.org/10.1111/psyp.12639

Lundqvist, D., Flykt, A., & Öhman, A. (1998). The Karolinska Directed Emotional Faces—KDEF *[CD-ROM]. Department of Clinical Neuroscience, Psychology section.* Stockholm, Sweden: Karolinska Institutet.

Moore, A., Gorodnitsky, I., & Pineda, J. A. (2012). EEG mu component responses to viewing emotional faces. *Behavioural Brain Research, 226*(1), 309–316. https://doi.org/10.1016/j.bbr.2011.07.048

Murphy, J., Brewer, R., Hobson, H., Catmur, C., & Bird, G. (2018). Is alexithymia characterised by impaired interoception? Further evidence, the importance of control variables, and the problems with the heartbeat counting task. *Biological Psychology, 136*, 189–197. https://doi.org/10.1016/j.biopsycho.2018.05.010

Nemiah, J. C., Freyberger, H., & Sifneos, P. E. (1976). Alexithymia: A view of the psychosomatic process. *Modern Trends in Psychosomatic Medicine, 3*, 430–439.

Niedenthal, P. M. (2007). Embodying emotion. *Science (New York, N.Y.), 316*(5827), 1002–1005. https://doi.org/10.1126/science.1136930

Pitcher, D., Garrido, L., Walsh, V., & Duchaine, B. C. (2008). Transcranial magnetic stimulation disrupts the perception and embodiment of facial expressions. *The Journal of Neuroscience, 28*(36), 8929–8933. https://doi.org/10.1523/JNEUROSCI.1450-08.2008

Ray, D., Bezmaternykh, D., Mel'nikov, M., Friston, K. J., & Das, M. (2021). Altered effective connectivity in sensorimotor cortices is a signature of severity and clinical course in depression. *Proceedings of the National Academy of Sciences of the United States of America, 118*(40), Article e2105730118. https://doi.org/10.1073/pnas.2105730118

Schachter, S., & Singer, J. (1962). Cognitive, social and physiological determinants of emotional state. *Psychological Review, 69*, 379–407.

Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology, 18*(4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486

Sel, A., Calvo-Merino, B., Tsakiris, M., & Forster, B. (2020). The somatotopy of observed emotions. *Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 129*, 11–22. https://doi.org/10.1016/j.cortex.2020.04.002

Sel, A., Forster, B., & Calvo-Merino, B. (2014). The emotional homunculus: ERP evidence for independent somatosensory responses during facial emotional processing. *Journal of Neuroscience, 34*(9), 3263–3267.

Sonnby-Borgström, M. (2009). Alexithymia as related to facial imitation, mentalization, empathy, and internal working models-of-self and-others. *Neuropsychoanalysis, 11*(1), 111–128.

Soussignan, R. (2002). Duchenne smile, emotional experience, and autonomic reactivity: A test of the facial feedback hypothesis. *Emotion, 2*(1), 52.

Teichmann, L., Moerel, D., Baker, C., & Grootswagers, T. (2022). An empirically driven guide on using Bayes factors for M/EEG decoding. *Aperture Neuro, 1*(8). https://doi.org/10.52294/82179f90-eeb9-4933-adbe-c2a454577289

van der Velde, J., Servaas, M. N., Goerlich, K. S., Bruggeman, R., Horton, P., Costafreda, S. G., & Aleman, A. (2013). Neural correlates of alexithymia: A meta-analysis of emotion processing studies. *Neuroscience and Biobehavioral Reviews,*

37(8), 1774–1785. https://doi.org/10.1016/j.neubiorev.2013.07.008

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40*(3), 655–664.

Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., … Gordon, E. (2004). Mapping the time course of nonconscious and conscious perception of fear: an integration of central and peripheral measures. *Human brain mapping, 21*(2), 64–74. https://doi.org/10.1002/hbm.10154.

Williams, L. M., Palmer, D., Liddell, B. J., Song, L., & Gordon, E. (2006). The "when" and "where" of perceiving signals of threat versus non-threat. *NeuroImage, 31*(1), 458–467. https://doi.org/10.1016/j.neuroimage.2005.12.009.