



Interindividual differences in interoception modulate behavior and brain responses in emotional inference

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ARTICLE INFO

Keywords:

Interoception
Emotion recognition
Emotional inference
Predictive coding

ABSTRACT

Emotional experiences are proposed to arise from contextualized perception of bodily responses, also referred to as interoceptive inferences. The recognition of emotions benefits from adequate access to one's own interoceptive information. However, direct empirical evidence of interoceptive inferences and their neural basis is still lacking. In the present fMRI study healthy volunteers performed a probabilistic emotion classification task with videotaped dynamically unfolding facial expressions. In a first step, we aimed to determine functional areas involved in the processing of dynamically unfolding emotional expressions. We then tested whether individuals with higher interoceptive accuracy (IAcc), as assessed by the Heartbeat detection task (HDT), or higher interoceptive sensitivity (IS), as assessed by the Multidimensional Assessment of Interoceptive Awareness, Version 2 (MAIA-2), benefit more from the contextually given likelihood of emotional valence and whether brain regions reflecting individual IAcc and/or IS play a role in this. Individuals with higher IS benefitted more from the biased probability of emotional valence. Brain responses to more predictable emotions elicited a bilateral activity pattern comprising the inferior frontal gyrus and the posterior insula. Importantly, individual IAcc scores positively covaried with brain responses to more surprising and less predictable emotional expressions in the insula and caudate nucleus. We show for the first time that IAcc score is associated with enhanced processing of interoceptive prediction errors, particularly in the anterior insula. A higher IS score seems more likely to be associated with a stronger weighting of attention to interoceptive changes processed by the posterior insula and ventral prefrontal cortex.

1. Introduction

Interoception is defined as the sense of internal physiological states of the body (Craig, 2002) and plays an important role in better understanding of emotional processes, and related to this, the emergence of mental disorders (Farb et al., 2015; Paulus and Stein, 2006; Seth, 2013a). As precursors to current theories of emotion processing, classical appraisal theories of emotions (James, 1884; Lange, 1885; Schachter and Singer, 1962) as well as the somatic marker hypothesis (Bechara et al., 2000; Damasio, 1996) have postulated early on that emotional experiences arise from the contextualized perception and interpretation of bodily responses to external stimuli. Building on and extending these theories on emotion processing, the interoceptive predictive coding model assumes that emotional content is determined by interoceptive predictions, meaning actively inferred predictive models of the causes of bodily sensations based on past experiences (Seth, 2013b; Seth and Friston, 2016). Interoceptive prediction errors, i.e., mismatches between descending interoceptive predictions and ascending primary interoceptive afferents, convey information about interoceptive changes

and activate corresponding (sympathetic or parasympathetic) systems to restore physiological homeostasis or allostasis (Seth and Friston, 2016; Seth et al., 2012). Accordingly, homeostatic and allostatic control is assumed to be anticipatory rather than reactive and rests on a model of the external world that includes interoceptive information and information received from physical and social domains of the environment (Stephan et al., 2016). The relative weight accorded to predictions and prediction errors at multiple levels of the predictive hierarchy is described in terms of *precision*, i.e. the reliability of (exteroceptive or interoceptive) signals (Friston, 2008, 2010). It has been proposed that individual differences in interoceptive precision also determine differences in the awareness of interoceptive sensations and, correspondingly, in emotional experience (Ainley et al., 2016).

Notably, interoception is of central importance not only for the perception of one's own emotional states, but also for those of other individuals (Ondobaka et al., 2017; Shah et al., 2017). Increased interoceptive abilities are linked to perceived arousal elicited by emotional stimuli (Dunn et al., 2010; Pollatos et al., 2005), higher sensitivity for emotional facial expressions of others (Cook et al., 2013; Terasawa et al., 2014)

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and a facilitation of the recognition of emotional changes, accompanied by a more precise adaptation to emotion probabilities (Hübner et al., 2021). Low interoceptive abilities on the other hand have been related to alexithymia, a subclinical phenomenon characterized by difficulties in identifying and describing feelings and associated with impaired expression recognition (Brewer et al., 2016; Cook et al., 2013; Herbert et al., 2011; Sowden et al., 2016). Nevertheless, there are different restrictive definitions and still no consensus on the exact conception of interoception. In this paper, we refer to a distinction based on various measures of interoceptive abilities according to Garfinkel (2015), differentiating between interoceptive accuracy (IAcc), operationalized as accuracy in detection of the heartbeat, interoceptive sensibility (IS) as self-reported measure regarding the individual evaluation of the ability to perceive body signals, and interoceptive awareness (IAw), defined as a metacognitive component in the sense of the degree of concordance between IS and IAcc.

The neuroanatomical brain regions involved in interoceptive processing extend from visceromotor areas (VMAs), through the insula cortex and the anterior cingulate cortex (ACC), to the orbitofrontal cortex (OFC), which is assumed to be situated at the top of the interoceptive hierarchy (Ainley et al., 2016; Barrett and Simmons, 2015; Garfinkel and Critchley, 2013; Seth and Friston, 2016). AIC, ACC and OFC have connections to hypothalamus, brain stem nuclei and spinal cord that presumably transmit allostatic predictions which modulate the set-points of homeostatic reflexes (Stephan et al., 2016). Regarding these interoceptive pathways, structurally and functionally closely connected insula and ACC are thought to be the most important cortical region activated by most interoceptive and affective stimuli (Ainley et al., 2016; Barrett and Simmons, 2015; Craig, 2009; Medford and Critchley, 2010; Menon and Uddin, 2010). In several studies, Wiebking and colleagues found correlations between insular interoceptive activity and depressive affect, as well as group differences during interoceptive awareness in the insula regions, with hypo-response of individuals with depression (Wiebking et al., 2011, 2015, 2014). Imaging studies provide evidence that these clusters are also involved in cerebral processing of emotions. For example, recent studies show overlaps of interoceptive signaling, emotion perception and social cognition, especially in the right anterior insular cortex (AIC) and frontotemporal regions (Pollatos et al., 2005; Zaki, Davis, & Ochsner, 2012; see Adolfs et al., 2017 for meta-analysis). Consequently, it can be assumed that increased cortical processing in these areas implies an advantage not only for the more accurate appraisal of one's own bodily signals, but that this better access to one's own interoceptive signals is also beneficial for recognizing the emotions of others.

In the present fMRI study, we aimed to investigate the impact of individuals' scoring in IAcc and IS on their brain activity and performance (reaction times) in a probabilistic emotion classification task. The experimental paradigm required participants to indicate whether a videotaped neutral facial expression develops into a happy or fearful expression. To introduce different levels of uncertainty, facial expressions varied in intensity at the end of the video. Moreover, we implemented different probabilities for the occurrence of happy or fearful faces per block to assess participants' propensity to efficiently update their predictive model. We quantified the different probabilities by information-theoretic measures, i.e., Shannon *surprise* (i.e., the improbability of an event) and *entropy* (i.e., the inverse predictability of a single stimulus), respectively, and modeled reaction times as well as the variability of BOLD amplitude as a function of surprise and entropy as parametric modulators (Shannon, 1948; Strange et al., 2005; see Methods for further details).

We tested whether individuals with higher IS or IAcc recognize others' emotions more easily and are more sensitive to learn from biased probabilities of emotional expressions. Here, it is important to emphasize that objective measures of IAcc are not necessarily correlated with subjective measures of IS (e.g., Ceunen et al., 2013; Forkmann et al.,

2016; Meessen et al., 2016). However, yet little is known about how interindividual differences in IS and IAcc affect emotion recognition. Our study is one of the first to directly examine how both measures affect emotion recognition. Based on the theoretical framework, we would initially assume that both higher IAcc and higher IS would have a beneficial effect on emotion recognition and context adaptation. In particular, we expected individuals with higher IS and IAcc to show lower thresholds for emotion recognition, reflected in decreased reaction times for emotional expressions (Hypothesis 1, H1). More specifically, based on the results from Hübner et al. (2021), we would assume that especially individuals with decreased IS are slower in recognizing more difficult conditions, i.e., low vs. high emotional intensity and fearful vs. happy valence of facial expressions. In addition, individuals with higher IS or IAcc should benefit more from a biased probability of an emotion, which is reflected in decreased reaction times for expected emotions (Hypothesis 2, H2) (see also Hübner et al., 2021).

On the neural level, we firstly investigated functional areas specialized in the processing of dynamically unfolding emotional facial expressions depending on intensity and valence. We expected high vs. low intensity of emotional expressions (Hypothesis 3, H3) to engage brain regions involved in the perception of changeable facial attributes and recognition of facial expressions, i.e., the inferior frontal gyrus (IFG), fusiform gyrus, insula and amygdala (Calder et al., 2003; Furl et al., 2010; Gallese et al., 2004; Haxby et al., 2002; Jung et al., 2021). For fearful vs. happy unfolding facial expressions, we expected increased neural activation especially in the amygdala (Adolphs et al., 1994; Breiter et al., 1996; Calder, 1996; Fusar-Poli et al., 2009). Secondly, regarding the probabilistic context adaptation, we expected stimulus-bound *surprise* to be positively correlated with activity in regions involved in the signaling of (interoceptive) prediction errors, i.e., AIC, ACC and striatum (Schiffer and Schubotz, 2011; Seth, 2013) (Hypothesis 4, H4), and *entropy* to be positively correlated with activity in the hippocampus, caudate nucleus, ACC, AIC and orbitofrontal cortex (OFC) (Ahlheim et al., 2014; Bechara et al., 2000; Herry et al., 2007; Schiffer, Ahlheim, Wurm, & Schubotz, 2012; Strange et al., 2005) (Hypothesis 5, H5). Finally, since especially the caudate nucleus is thought to be associated with perceptual prediction errors (Schiffer and Schubotz, 2011; Schiffer et al., 2012), we expected that participants' IAcc and IS correlates positively with activation in the caudate nucleus, as well as insula and ACC (i.e., brain regions related to interoceptive processing and signaling of (interoceptive) prediction errors), when confronted with less predicted or less predictable emotions (Hypothesis 6, H6).

2. Materials and methods

2.1. Participants

Forty-two right-handed healthy young volunteers ($M_{\text{age}} = 21.00$ years, $SD = 2.51$, age range = 18-29 years, 34 women, 8 men) with normal or corrected-to-normal vision were included in the present study. None of them reported a history of neurological or psychiatric disorders and all participants met the criteria for MRI scanning. The study protocol was conducted in accordance with ethical standards of the Declaration of Helsinki and approved by the Local Ethics Committee of the University of Muenster. Each participant submitted a signed informed consent form and received either reimbursement or course credits for their participation afterwards. Individuals provided written informed consent to permit for all potentially identifying information to be published.

2.2. Stimulus material

The emotional stimuli used were the same as reported in Hübner et al. (2021) and consisted of short videos with a mean duration of 3.00 s, displayed on a grey background. In order to avoid ceiling

effects due to noticeable features like the hairline, in this task we additionally extended the grey background ellipsoid around the emotional faces. To create valid stimuli which are comparable to facial expressions that one encounters in daily life, we accepted that the emotional videos would slightly vary in length ($SD = 0.39$). However, to control for possible confounds of these variations on the participants' reaction time, we included the video durations as a covariate in our analyses. We created videos with female or male faces posing from neutral expressions to happy or fearful emotional ones. To introduce different levels of uncertainty, emotional facial expressions differed in terms of INTENSITY (high/low). Moreover, we controlled for potential effects of mouth opening on emotion recognition (Langeslag, Gootjes, & van Strien, 2018). To this end, each condition (fearful/happy expressions of high/low intensity) was presented with the mouth open and closed, i.e., in two different versions. However, to reduce the complexity of the statistical model, we did not include these conditions in the statistical analyses. A detailed explanation of the generation of the stimuli used is described in Hübner et al. (2021).

2.3. Task

During the main task in the MR scanner, the videos were centrally back-projected onto a screen. Participants viewed the screen through a mirror above the head coil. Videos were presented separated by jittered inter-stimulus-intervals (ITI) of 3500, 4000, 4500 or 5000 msec, during which a fixation cross was displayed centrally on the screen. The participants were asked to watch the presented videos attentively and to respond as fast and accurately as possible as soon as they recognized the emotion in the emotional condition of a presented face. Participants responded by pressing one of two response keys with their right index and middle finger. Stimulus-response mappings were counterbalanced across participants. The task consisted of 16 emotional blocks with 16 consecutive videos each, i.e., a total of 256 trials. Thus, each of the 128 videos was shown twice. After each block, participants had a short break of 8 s, during which participants were given the information that the block has ended, followed by information regarding the start of a new block and instructions on key assignment. Accordingly, the overall task lasted about 33 min (2624 sec).

Within each block, either a high (75%) or low (25%) probability for the occurrence of fearful or happy faces was implemented. Stimuli were presented in a pseudo-randomized order ensuring that each of the eight conditions (happy vs. fearful x high vs. low intensity x mouth open vs. closed) was shown twice in each block and videos of one actor/actress were never repeated across consecutive trials. Transitions between the block types were balanced across the experiment. The randomization was programmed using MATLAB R2019b (The MathWorks Inc., Natick, MA, USA) and stimuli were presented using the Presentation software (Version 19.0, Neurobehavioral Systems, Inc., Berkeley, CA). A schematic diagram of the task is shown in Fig. 1.

Prior to the experiment, participants performed a short training session to get accustomed to the task. The training consisted of one block of 16 trials each and an equal probability for the different conditions.

2.4. Assessment of interoceptive sensibility (IS) and interoceptive accuracy (IAcc)

For the self-assessment of interoceptive sensibility (IS) we used the Multidimensional Assessment of Interoceptive Awareness, Version 2 (MAIA-2, Mehling et al., 2018). This questionnaire quantifies the self-reported belief of the perception of one's own bodily signals. The MAIA-2 is a state-trait questionnaire with 37 items consisting of the following eight subscales: noticing, i.e., the awareness of uncomfortable, neutral or comfortable body sensations; not-distracting, i.e., the tendency to ignore or distract oneself from sensations such as pain or discomfort; not-worrying, i.e., emotional distress or worry regarding sensations of pain or discomfort; attention regulation, i.e., the ability to control attention

to the sensations of the body; emotional awareness, i.e., the awareness of the connection between body sensations and emotional states; self-regulation, i.e., the perceived ability to regulate distress by attention to body sensations; body listening, i.e., how one's actively listens to the body for insight, and trust, i.e., the experiences of the body as safe and trustworthy (Mehling et al., 2012). Participants have to indicate how often each statement applies to them in everyday life on a 5-point Likert scale from 0 (*never*) to 5 (*always*). The validity of the MAIA-2 scales is indicated with Cronbach's alpha ranging from 0.64 to 0.83 for the eight scales (Mehling et al., 2018). For our statistical analyses, we calculated a total score per participant by summing up the results of the subscales. Together with other questionnaires assessing the participants' emotion processing, the MAIA-2 was completed online by the participants in the using the academic Unipark program (Questback GmbH, 2017).

For the assessment of interoceptive accuracy (IAcc) we used the Heartbeat detection task (HDT) as reported in Terasawa et al. (2014) based on a task developed by Schandry (1981) and Ehlers & Breuer (1992). The HDT task was assessed in a second session on average five days after the main MR session. Instructions were given on a screen using the presentation software (Version 19.0, Neurobehavioral Systems, Inc., Berkeley, CA). The intervals were marked by a short start and end tone. During the HDT, the participants were asked to count their own heartbeat at different time intervals. Participants were asked to estimate the frequency of heartbeats solely by focusing on bodily sensations and were instructed not to predict their heart rate. A pulse oximeter was placed gently on the fingertips so that participants could not feel the pressure of their pulse. Participants sat in a comfortable chair and were instructed not to touch any part of their body during the task. The real heartbeats were recorded using the pulse oximeter and extracted using the Brain Vision Recorder software (Version 1.20.0801; Brain Products GmbH, 2018). The present study included a total of six intervals with a duration of $2 \times 35s$, $2 \times 25s$ and $2 \times 45s$ (see Terasawa et al., 2014). For each trial, an accuracy score was derived using the following formula presented in Garfinkel et al. (2015):

$$1 - \left(\left| nbeats_{real} - nbeats_{reported} \right| \right) / \left((nbeats_{real} + nbeats_{reported}) / 2 \right)$$

The resulting accuracy scores were averaged over the six trials, yielding an average value for each participant varying between zero and one, with higher values indicating higher interoceptive accuracy (Hartel et al., 2013).

2.5. fMRI data acquisition

Whole-brain imaging data were collected with a 3-T Siemens Magnetom Prisma MR tomograph (Siemens, Erlangen, Germany) using a 20-channel head coil. To acquire structural data for each participant a 3D-multiplanar T1 weighted gradient-echo (MPRAGE) sequence was used. Scanning parameters were set to 192 slices, a $256 \times 256 \text{ mm}^2$ field of view (FoV), a repetition time (TR) of 2.28 msec, an echo time (TE) of 2.28 msec and slice thickness of 1 mm.

Functional blood oxygenation level-dependent (BOLD) images were acquired using a T2*-weighted single-shot echo planar imaging (EPI) sequence (64×64 data acquisition matrix, 192 mm field of view (FoV), 90° flip angle, time of repetition (TR) = 2000 ms, echo time (TE) = 30 msec). Each volume consisted of 33 adjacent axial slices with a slice thickness of 3 mm and a gap of 1 mm, resulting in a voxel size of $3 \times 3 \times 4 \text{ mm}$. To provide a whole brain coverage the images were acquired in ascending order with scanning axis tilting 20 degrees up the AC-PC plane in order to lessen signal dropouts in orbitofrontal regions. In order to minimize head motion, the head was tightly fixated with cushions. Stimuli were projected on a screen positioned behind the scanner bore and presented in the center of the field of vision by a video projector. The subjects viewed the screen by a 45° mirror, which was fixated on the top of the head coil and adjusted for each participant to provide a good view of the entire screen.

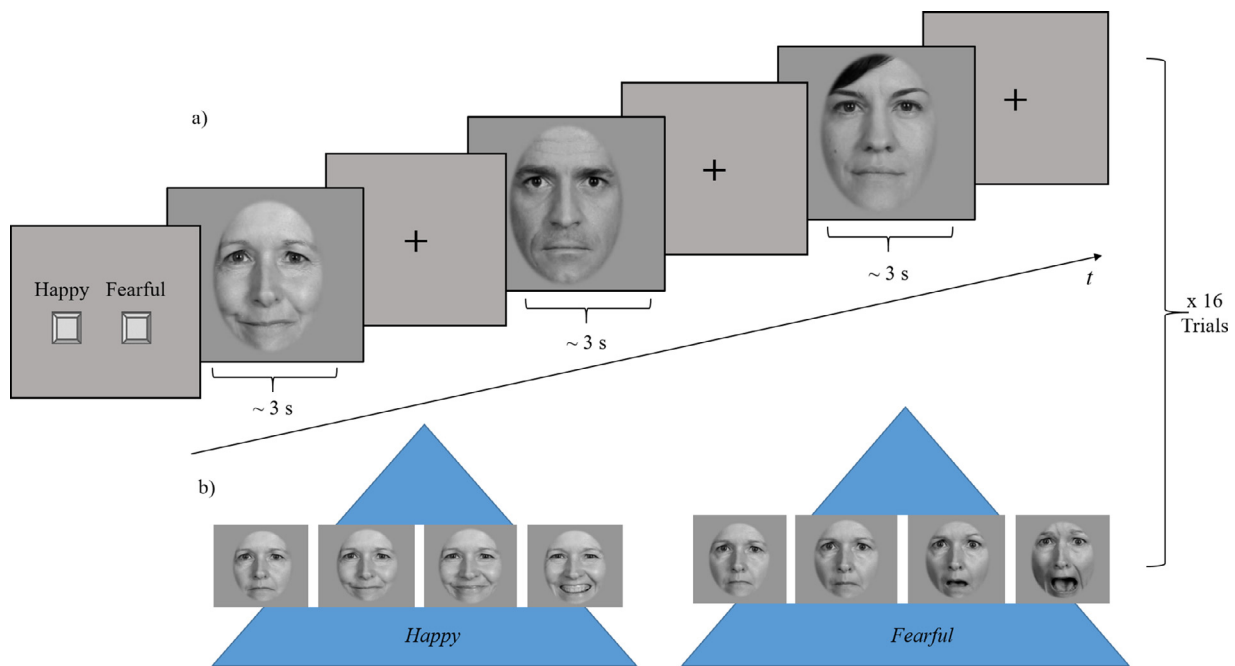


Fig. 1. Schematic diagram of the task. (a) At the beginning of each block, instructions indicate that the participant has to indicate the emotion of the upcoming faces (happy vs. fearful). One block includes 16 consecutive video trials. (c) Videos depict actors/actresses posing from neutral to either happy or fearful facial expressions. The actor and actresses in the figure have given written informed consent to publish the photographs.

2.6. Behavioral data analysis

Basic statistical analyses were performed using R, version 3.6.2 (R Core Team, 2019). Behavioral performance was measured in terms of reaction times (RTs). We restricted the behavioral analyses to RTs, since false alarms and missing data accounted for only 4.92 % of the data. Incorrect or missing responses were excluded from analyses. For the comparisons of RTs, we tested whether VALENCE, INTENSITY and information-theoretic quantities, i.e., Shannon's surprise $I(x_i)$ and entropy $H(X)$ (Shannon, 1948), could predict (variance in) RTs on a single-trial level. While 'surprise' measures the improbability of a particular event, 'entropy' measures the expected or average surprise over all events and thus reflects the predictability of a stimulus in a given context (Strange et al., 2005). For our analysis, we based Shannon's surprise on the frequency of a trial of a certain valence x_i normalized by the sum of all past trials in the block:

$$p(x_i) = \frac{n(x_i) + 1}{\sum x_i + 1}$$

For the two factor levels of valence (happy, fearful), prior counts before observing the first trial in a block were set to $\frac{1}{2}$. The surprise $I(x_i)$ of each stimulus measures the amount of information provided by the current stimulus. This is given by the negative logarithm of the probability:

$$I(x_i) = -\ln p(x_i)$$

Entropy $H(X)$ is given by the average surprise of all possible outcomes. As illustrated in the following formula, it quantifies the expected information of an event regarding its predictability:

$$H(X) = \sum_i -p(x_i) \ln p(x_i)$$

We conducted generalized linear mixed-effects analyses using R, version 3.6.2 (R Core Team, 2019) via the package *lme4*, version 1.1.21 (Bates et al., 2015). We transformed RTs to the natural logarithm in order to achieve a more closely approximate to normal distribution. For the factors VALENCE and INTENSITY effect coding was used, with -1 for

happy and 1 for fearful expressions, and 1 for high and -1 for low intensity expressions. While surprise and entropy were centered at individual levels, the MAIA-2 score and HDT score was centered at group level. Each model was fit with VALENCE and INTENSITY (and their interaction), Shannon's surprise and entropy and their respective interaction with the MAIA-2 score and the HDT score separately as fixed effects, and with a random intercept for each subject. As discussed above, we added video duration to the statistic models to control for potentially confounding effects of varying video length on RTs. In accordance with our assumptions and our previous work, video length did not predict RTs, $b = 0.000$, $\beta = 0.000$, $t = 1.004$, $p = 0.315$. Statistical significance for each fixed effect was calculated via *lmerTest*, version 3.1.1 (Kuznetsova et al., 2016), using the Satterthwaite's approximation to denominator degrees of freedom. The significance level was set to $\alpha = .05$.

2.7. fMRI data preprocessing

All brain image preprocessing and basic statistical analyses were performed with SPM12 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) and custom Matlab scripts (Version R2020b; The MathWorks Inc., Natick, MA, USA). To correct for differences in slice acquisition time, all functional images were slice-timed to the middle slice. All individual functional MR (EPI) images were realigned to correct for three-dimensional motion. Structural images were co-registered (rigid body transformation) to the mean functional image and then segmented into native space tissue components. Functional images were then normalised to the standard MNI space (Montreal Neurological Institute, Montreal, QC, Canada) and spatially smoothed with a Gaussian kernel of full width at half-maximum of 6mm^3 . Motion correction estimates were inspected visually. Seven participants showed head movements in the range of 3 to 4 mm. In order to decide whether these datasets should be excluded, we checked each subject's data for motion artifacts after applying motion correction. In addition, we compared the group results with and without the respective subjects, revealing no qualitative differences in the effects apart from a loss of statistical power in the case of reduced group size. Accordingly, we excluded only data sets with visible motion artifacts who exceeded a maximum of 4 mm head move-

ments between two scans in the x, y, and z dimensions, resulting in the exclusion of three participants.

2.8. fMRI design specification

The statistical analysis of functional images was conducted using SPM12 implementing a general linear model (GLM) for serially autocorrelated observations (Friston et al., 1995; Worsley and Friston, 1995). To investigate functional areas specialized in the processing of emotion recognition depending on INTENSITY and VALENCE, a GLM was constructed including four regressors coding for onsets and durations of the specific event types, i.e., happy high (hh), happy low (hl), fear high (fh) and fear low (fl), which were then convolved with the canonical hemodynamic response function (HRF) and regressed against the observed fMRI data. To model variability in the BOLD amplitude as a function of surprise and entropy, additional to each of the four regressors two parametric modulators each were added i.e., one for surprise and one entropy. Each of these modulators were mean-centered before entering the GLM. The subject-specific six rigid-body transformations obtained from realignment were included as regressors of no interest.

On the first level, one-sample *t*-tests for the following contrasts were calculated and submitted to a second-level *t*-test to detect functional areas specialized in the processing of emotion recognition on group level: intensity high (hh \cap fh) > intensity low (hl \cap fl), fearful (fh \cap fl) > happy (hh \cap hl), as well as the respective opposing contrast, i.e., intensity low (hl \cap fl) > intensity high (hh \cap fh), happy (hh \cap hl) > fearful (fh \cap fl), and parametric effects of surprise and entropy for all trials (fearful \cap happy). For second-level whole-brain analyses, statistical differences were defined as $q < .05$ at the cluster level following False Discovery Rate (FDR) correction. Moreover, we defined regions of interest (ROIs) to correlate BOLD activation of the selected contrasts with differences in interoceptive abilities, i.e., interoceptive sensibility (IS, assessed by MAIA-2) and interoceptive accuracy (IAcc, assessed by HDT). We defined hypothesized ROIs of the anterior cingulate cortex (ACC) and insula, as well as caudate nucleus. All ROIs were derived from the automated anatomical labelling (AAL) atlas and created using the SPM Wake Forest University (WFU) Picketatlas toolbox (<http://www.fmri.wfubmc.edu/cms/software>, version 2.3) (Maldjian et al., 2003). We then used these ROIs to extract each subject's beta values of the activity associated with the defined contrasts during the task, i.e., VALENCE, INTENSITY, SURPRISE and ENTROPY. We performed correlation analyses using SPSS 26 (IBM, New York, USA) to examine the relationship between BOLD activation of the selected contrasts and interoceptive abilities, with an α -level of $p < .05$, two-tailed.

3. Results

3.1. Behavioural results

Emotion recognition. As consistently reported in other studies, IS (i.e., continuously varying MAIA-2 total scores) and IAcc (i.e., individual HDT score) did not significantly correlate, $r = 0.001$, $p = 0.995$. In line with our hypothesis, the linear mixed-effect model predicting RTs revealed a significant main effect of valence, $b = 0.14$, $\beta = 0.007$, $t = 17.67$, $p < 0.001$, with increased RTs for fearful facial expressions compared to happy ones, and a main effect of INTENSITY, $b = -0.05$, $\beta = 0.007$, $t = -6.51$, $p < 0.001$, driven by increased RTs for low vs. high intensity of an expression. In contrast to Hübner et al. (2021), no significant interaction between VALENCE and INTENSITY was found, $b = -0.01$, $\beta = 0.01$, $t = -1.16$, $p = 0.247$.

Contrary to our hypothesis, the linear mixed-effect model predicting RTs revealed no significant main effects of individuals' IS, $b = 0.00$, $\beta = 0.001$, $t = 0.02$, $p = 0.986$, or IAcc, $b = 0.09$, $\beta = 0.065$, $t = 1.44$, $p = 0.15$. However, we found a significant interaction between VALENCE and IS, $b = 0.001$, $\beta = 0.004$, $t = 2.106$, $p = 0.03$, as well as between VALENCE and IAcc, $b = -0.085$, $\beta = 0.027$, $t = -3.085$, $p = 0.002$. In accor-

dance to Hübner et al. (2021), with increasing IS, participants showed significantly longer RTs for fearful faces, but not for happy ones. In contrast to what we would have expected, with increasing IAcc participants showed significantly longer RTs for recognizing happy faces; this effect did not occur for fearful faces (Fig. 2a, b).

Probabilistic context adaptation. We tested whether Shannon's surprise and entropy of a single emotional expression in interaction with individual IS and IAcc were predictive of the participants' performance. The linear mixed-effect model predicting RTs revealed a significant main effect of surprise, $b = -0.014$, $\beta = 0.004$, $t = -3.258$, $p = 0.001$, and entropy, $b = 0.048$, $\beta = 0.024$, $t = 2.003$, $p = 0.04$. This effect was driven by increasing RTs with increasing entropy and decreasing RTs with increasing surprise. Regardless of differences in IS or IAcc, participants showed longer RTs to less predictable events, but shorter RTs to more surprising events, corresponding an expected positive correlation of entropy and RTs, as well as an unexpected negative correlation of surprise and RTs, respectively. Furthermore, we found a significant interaction between IS and entropy, $b = 0.002$, $\beta = 0.001$, $t = 2.138$, $p = 0.032$. As expected, only for participants with high IS, but not for those with low IS, entropy was positively correlated with RTs (Fig. 3). Finally, there were no significant interactions for IS and surprise or IAcc and surprise or entropy (all $p > 0.31$).

3.2. fMRI results

Main effects of emotional valence and intensity. The contrast between high and low emotional intensity [(hh \cap fh) > (hl \cap fl)] revealed significant bilateral activation in the inferior occipital gyrus, as well as unilateral activation in the fusiform gyrus (Fig. 4a, Table 1). For the reverse contrast [(hl \cap fl) > (hh \cap fh)] (Fig. 4b), the analysis revealed higher frontal activations exclusively in the right hemisphere, including middle frontal gyrus, supplementary motor area, and anterior dorsal insula (Table 1). To identify the network associated with emotional valence, we contrasted fearful faces (fh \cap fl) with happy faces (hh \cap hl), which revealed significant bilateral activation in the temporal lobe, as well as the inferior frontal gyrus (IFG) and the anterior insula (Table 1, Fig. 4c). No significant activation for the reverse contrast [(hh \cap hl) > (fh \cap fl)] was found.

Parametric effects of surprise and entropy. Corresponding with our hypothesis, we ran parametric analyses capturing regions more activated during more surprising events (positive surprise) as well as increased activation for events with decreasing predictability (positive entropy). We further modelled the respective reverse contrasts, i.e., negative surprise and negative entropy. For negative surprise and positive entropy, however, no significant activation could be observed. For more surprising events, we found significant unilateral activation in the left postcentral gyrus (Table 2, Fig. 5b). The brain response to more predictable events (i.e., negative entropy) showed a bilateral activity pattern comprising - amongst others - the inferior frontal gyrus (IFG), posterior insula and middle temporal gyrus (Table 2, Fig. 5a).

ROI activation relating to interoceptive sensibility (IS) and interoceptive accuracy (IAcc). We correlated each participant's MAIA-2 total score and HDT score with the extracted beta values of the defined contrasts for the following regions of interest (ROIs): ACC and insula for all contrasts; caudate nucleus in addition for the parametric effects of surprise and entropy, as this region has repeatedly found to be activated by perceptual prediction errors (Schiffer and Schubotz, 2011; Schiffer et al., 2012). For the MAIA-2 score as a measurement of IS, no significant correlations could be found (all $p > 0.294$). For an explorative analysis and to offer a basis for further research in the area, a table with significant correlations of the eight MAIA-2 subscales with the extracted beta weights is provided in the Supplementary material (Table S1).

Regarding differences in interoceptive accuracy (IAcc), parameter estimates of the right ACC activity for the contrast VALENCE (Fearful vs. Happy) marginal significantly correlated with the HDT score of the participants ($r = 0.282$, $p = 0.071$, two-tailed). Activity of ACC or insula for

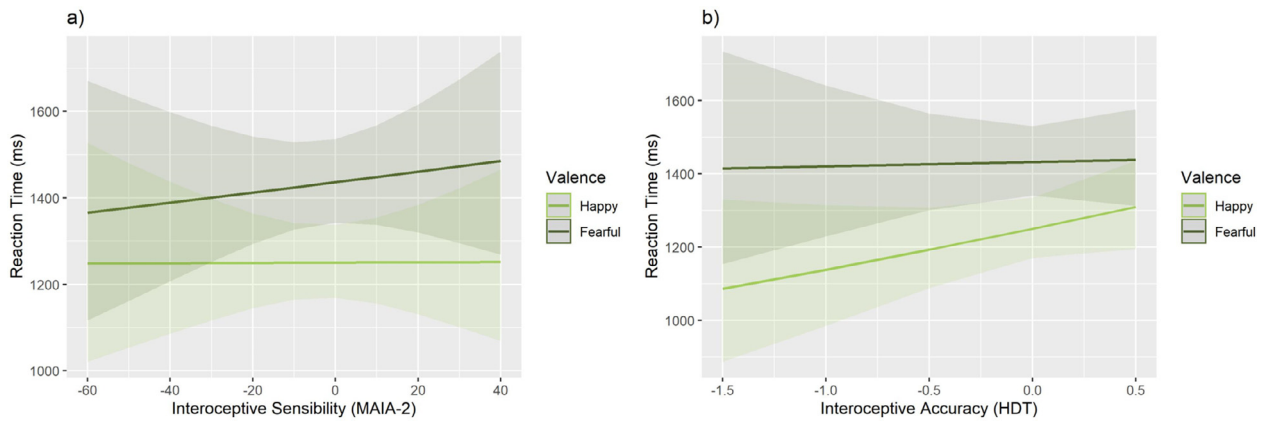


Fig. 2. Significant effects of (a) interoceptive sensitivity assessed by the MAIA-2 questionnaire (Mehling et al., 2018) and (b) interoceptive accuracy assessed by HDT-score, on reaction time divided for VALENCE (happy, fearful)

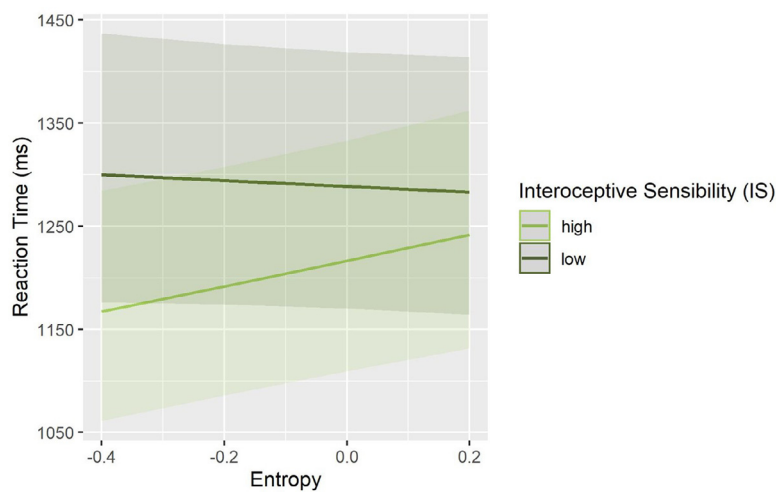


Fig. 3. Results of the linear mixed effect regression model predicting reaction time (ms) by mean-centered entropy as a function of interoceptive sensitivity (IS) assessed by the MAIA-2 questionnaire (Mehling et al., 2018). For illustrative purposes, we performed a median split to divide participants into two discrete groups with high and low IS. The solid lines depict the regression fit, and the shaded areas show the 95% confidence intervals.

Table 1

Maxima of activation from the conjunction analysis of the contrast images of Intensity high > Intensity low, Intensity low > Intensity high and Fearful > Happy at $p < 0.05$ cluster-level FDR-corrected. Labels are reported according to the AAL atlas.

Region Label	Cluster Extent	t-value	MNI Coordinates		
			x	y	z
<i>Intensity high > Intensity low</i>					
Right Inferior Occipital Gyrus	827	9.98	45	-70	2
Right Fusiform Gyrus		6.59	39	-58	-13
Left Inferior Occipital Gyrus	579	8.82	-45	-79	5
Left Middle Occipital Gyrus		7.36	-27	-94	14
<i>Intensity low > Intensity high</i>					
Right Middle Frontal Gyrus	295	4.93	30	50	8
Right Superior Frontal Gyrus	83	4.93	15	11	50
Right Anterior Cingulate Cortex		3.80	9	23	29
Right Supplementary Motor Area		3.67	9	23	53
Right Anterior Insula	84	4.63	36	17	11
<i>Fearful > Happy</i>					
Right Superior Temporal Gyrus	515	6.79	48	-43	17
Left Cerebellum	802	6.35	-6	-76	-31
Left Middle Temporal Gyrus	141	5.83	-57	-52	11
Left Anterior Insula	284	5.81	-27	23	2
Left Inferior Frontal Gyrus (p. Triangularis)		4.69	-45	23	20
Left Inferior Frontal Gyrus (p. Orbitalis)		4.59	-48	11	20
Right Anterior insula	508	5.49	36	23	-4
Right Inferior Frontal Gyrus (p. Orbitalis)		5.49	45	20	5
Right Precentral Gyrus		5.18	48	5	47
Left Precentral Gyrus	141	5.29	-33	-25	53
Right Supplementary Motor Area	225	5.01	6	17	53
Left Superior Parietal Lobule	73	4.32	-30	-52	41

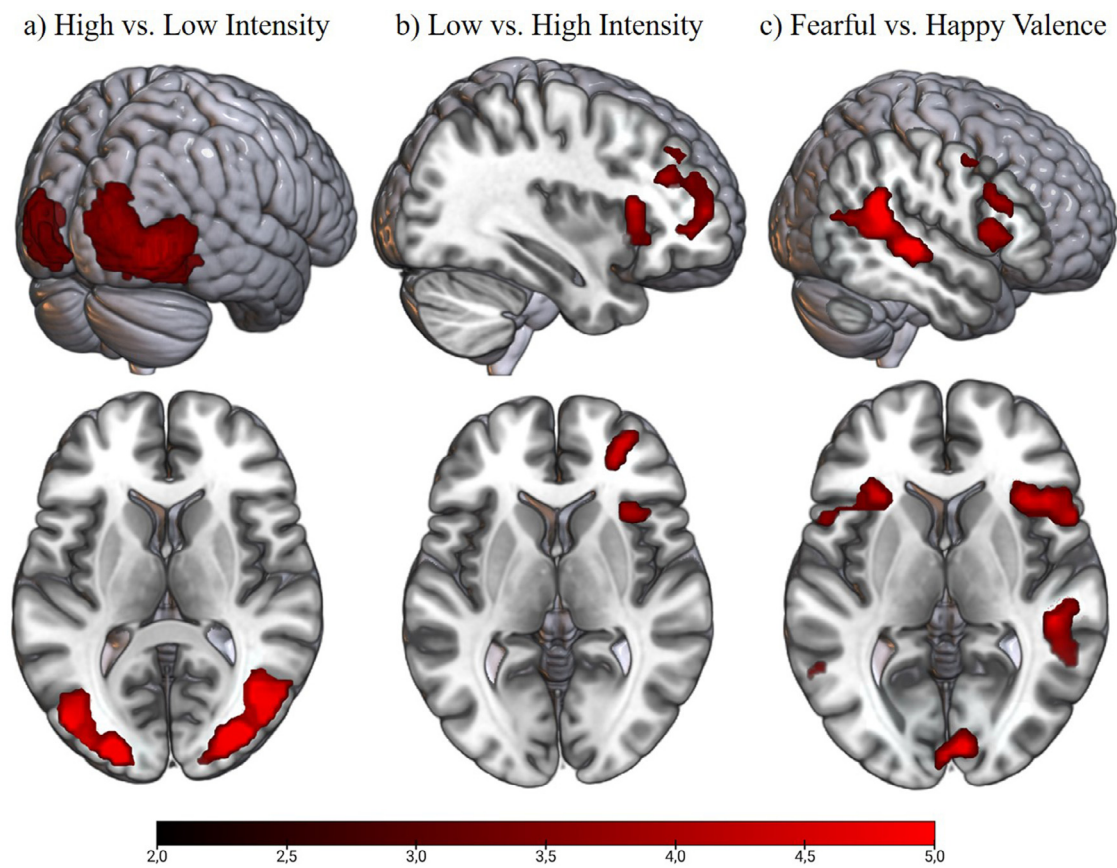


Fig. 4. fMRI main effects at $p < .05$, whole-brain FDR cluster-corrected. (a) There was statistically significantly increased activation during high vs. low emotional intensity in the inferior occipital gyrus, as well as unilateral activation in the fusiform gyrus. (b) Low vs. high intensity of emotions elicited significant activation in frontal regions, comprising right-hemispheric activation of the right frontal gyrus, ACC and anterior insula. (c) Fearful vs. happy faces increased activation (amongst others) in the temporal cortex as well as the inferior frontal gyrus and anterior insula. Note: Since no significant activation was found, the reverse contrast happy > fearful faces is not displayed in the Figure.

Table 2

Maxima of activation from the conjunction analysis of the parametric effect images of *surprise positive* and *entropy negative* at $p < 0.05$ cluster-level FDR-corrected. Labels are reported according to the AAL atlas.

Region Label	Cluster Extent	t-value	MNI Coordinates		
			x	y	z
<i>Surprise positive</i>					
Left Postcentral Gyrus	173	7.17	-33	-28	44
Left Superior Parietal Lobule	57	6.47	-30	-46	56
<i>Entropy negative</i>					
Left Middle Frontal Gyrus	1797	7.17	-42	50	-7
Left IFG (p. Orbitalis)		6.84	-45	26	-10
Left IFG (p. Triangularis)		6.47	-42	38	-4
Right Precentral Gyrus	207	6.13	36	-22	53
Right Posterior insula	313	5.77	36	-19	20
Right Middle Temporal Gyrus		5.61	66	-31	-1
Left Middle Temporal Gyrus	131	5.36	-63	-37	-7
Left Medial Frontal Cortex	48	5.14	-6	47	-13
Left Posterior insula	36	5.09	-33	-28	23
Left Angular Gyrus	175	5.05	-48	-64	38
Right Cerebellum Crus 1	208	4.95	33	-76	-31
Right Postcentral Gyrus	68	4.57	57	-7	41
Right IFG (p. Orbitalis)	49	4.57	42	32	-10
Right IFG (p. Triangularis)		4.13	51	41	-7
Right Precuneus	42	3.89	6	-58	35

the contrast of INTENSITY were not related to differences in the HDT (all $p > 0.81$). For the parametric effects of entropy, parameter estimates of left ($r = .330$, $p = .033$, two-tailed) and right caudate activity ($r = 0.362$,

$p = 0.018$, two-tailed) as well as (marginal) left insula activity ($r = 0.299$, $p = 0.054$, two-tailed) significantly correlated with the HDT scores, i.e., individuals with greater IAcc showed significantly higher activation in caudate and tendentially also in left insula for the occurrence of less predictable events (Fig. 6a, b). Consistent with these findings, beta weights of ROI activity in left caudate for the surprise contrast were also significantly correlated to interoceptive accuracy ($r = 0.356$, $p = 0.021$; right caudate $r = 0.285$, $p = 0.067$, two-tailed) (Fig. 6c).

4. Discussion

In the current fMRI study, we investigated whether an individual's interoceptive sensibility (IS) and interoceptive accuracy (IAcc) are related to the speed of recognizing emotional changes in facial expressions of others, and if so, whether this relation depends on the valence, intensity and current probability of emotions. Furthermore, we investigated the neural basis of dynamically unfolding emotional expressions and interoceptive abilities.

Individuals' IS and IAcc had no effect on the speed of detecting the emergence of emotional expression, but interestingly, these parameters differed with regard to their impact on recognizing emotional valence. On the neural level, both valence and intensity of emotion had distinct effects on different brain sites including, among others, the anterior insula cortex (AIC) and the frontal lobes. Participants with higher IS recognized facial emotions faster when they were statistically more likely, whereas no such effects emerged for IAcc. Independent of IS and IAcc, more predictable emotions elicited bilateral brain activity in the IFG and the posterior insula. Finally, as expected, participants' IAcc corre-

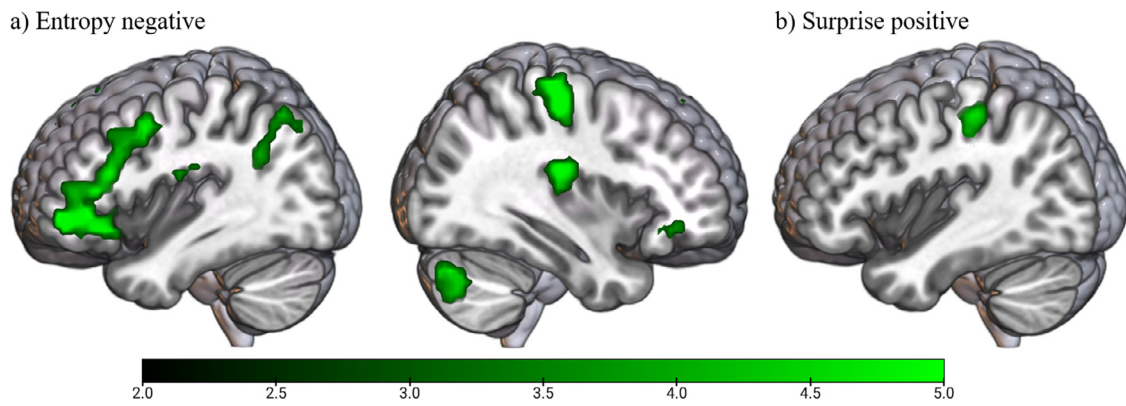


Fig. 5. fMRI results at $p < 0.05$, whole-brain FDR cluster-corrected for the parametric effects of surprise and entropy. (A) Decreasing entropy (i.e., negative entropy) elicited significant bilateral activity pattern comprising - amongst others - the IFG, the left posterior insula as well as the middle temporal gyrus. (B) Shown is the statistically significant increased activation with increasing surprise of an emotion (i.e., positive surprise), with unilateral activation in the postcentral gyrus.

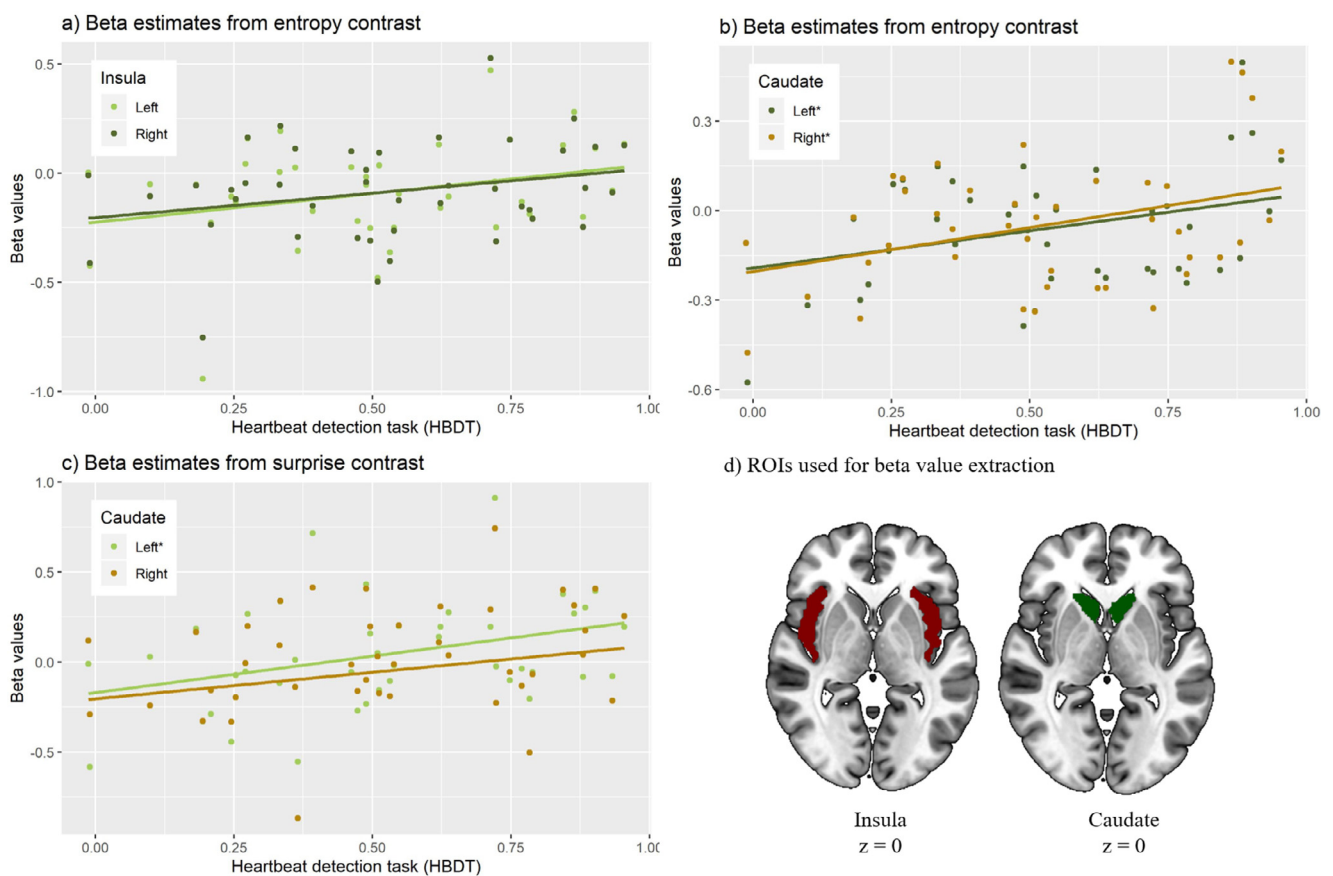


Fig. 6. Region of interest (ROI) fMRI data and beta value extraction for entropy and surprise contrast. (a) Activation for differences of the predictability of emotions (entropy) scaled with participants' interoceptive accuracy (IAcc) as indicated by HDT score. Left ($r = 0.330, p = 0.033$, two-tailed) and right caudate activity ($r = 0.362, p = 0.018$, two-tailed) significantly correlated with the HDT scores. (b) Marginal significant correlation of HDT and parameter estimates of the left insula activity ($r = 0.299, p = 0.054$, two-tailed) for beta estimates of the entropy contrast. (c) Significant correlation of beta estimates of the left caudate in the surprise contrast with interoceptive accuracy ($r = 0.356, p = 0.021$; right caudate $r = 0.285, p = 0.067$, two-tailed). (d) Insula and caudate ROI used for beta value extraction.

lated positively with activation in the caudate nucleus and insula when confronted with less predicted or less predictable emotions.

4.1. Recognizing emotional changes with different interoceptive abilities: the effect of valence and intensity

Our behavioral results partly confirmed the hypothesis that IS and IAcc modulate the recognition of emotional changes in facial expressions of others. Contrary to Hübner et al., (2021), higher IS scores were not

associated with lower thresholds for emotional change recognition, and individuals with lower IS did not benefit more from high intensities of facial emotions. In the present study, we added IAcc as an objective measure of interoceptive abilities but could not find any corresponding evidence for a generally lower detection threshold or interaction with intensity of emotions either.

Regarding the recognition of emotions with different valences, happy faces were recognized faster than fearful faces. This is in line with consistent evidence for superior recognition of happy faces compared to

other facial expressions (Ekman, 1982; Hess et al., 1997; Kirita and Endo, 1995; Leppänen and Hietanen, 2003; Palermo, 2004), and may be due to the fact that happiness requires simpler physical changes and occurs more frequently in daily life (Adolphs, 2002; Leppänen and Hietanen, 2003; Montagne et al., 2007).

Interestingly, differences in IS and IAcc interacted with emotional valence, indicating that individuals with high vs. low IS showed longer RTs for fearful faces, but not for happy ones, whereas with high vs. low IAcc individuals showed increased RTs for happy ones. Previous studies suggested that interoceptive abilities facilitate the sensitivity to recognize others' emotions (Hübner et al., 2021; Terasawa et al., 2014). Yet, there is evidence suggesting that individuals with higher IAcc are less accurate in recognizing negative emotions, which has been explained by the fact that with increasing IAcc, emotions are more regulated (Georgiou et al., 2018). Accordingly, the ability to regulate interoceptive signals by weighting of attention might lead to interindividual differences in emotion recognition. This could also serve as an explanation for the observed contrasting interactions between IS and IAcc and emotional valence, as will be discussed further below.

As hypothesized, high vs. low intensity of emotional expressions revealed significant activation in the inferior occipital gyri and in the right fusiform gyrus. The processing of emotional face features is proposed to involve pathways from inferior occipital gyrus to fusiform gyrus, comprising the fusiform face area (FFA), which is known as a central region in the face-selective cortical network (Goffaux et al., 2013; Grill-Spector et al., 2004; Richler and Gauthier, 2014). Thereby, the inferior occipital gyrus is proposed to be involved in early visual processing and basic perception of facial features, whereas the fusiform gyrus processes the identity of the faces (Haxby et al., 2000). Recently, the fusiform gyrus was found to show enhanced activation during emotionally arousing stimuli (Frank et al., 2019) and fusiform volume was found to be positively correlated with performance in emotional intensity recognition (Jung et al., 2021). Moreover, Sato et al. (2004) found increased activation in the inferior occipital gyrus and fusiform gyrus for dynamic compared to static emotional facial expressions. In line with these studies, we suggest that the observed increased activity for high vs. low intensity of emotional expressions is related to enhanced perceptual processing for dynamic characteristics of faces.

In contrast, low vs. high emotional intensity elicited higher activation in the right middle frontal gyrus, right ACC, right supplementary motor area and anterior dorsal insula. It can be assumed that the detection of low- compared to high-intensity emotions is more difficult and requires a more detailed evaluation. The dorsolateral prefrontal cortex (dlPFC) is proposed to play a key role in attentional processing of emotional information (Mondino et al., 2015) and to contribute to the distinction of the specific emotion that is expressed (Tsuchida and Fellows, 2012). Impairment of the dlPFC and ACC have been associated with deficits in interpersonal perception (Mah et al., 2004), for example becoming evident in patients suffering from behavioral variant frontotemporal dementia (bvFTD) (Hübner et al., 2022; Keane et al., 2002). The observed increased activation in the anterior dorsal insula also supports the assumption of more profound evaluative processing of emotions with low intensity, as this area plays a crucial role in the integration of affective and evaluative processes (Berntson et al., 2011). More specifically, the AIC has been linked to emotion recognition by modulating arousal potentially mediated through interoceptive inferences (Motomura et al., 2019).

Correspondingly, we also observed increased AIC and IFG activation for fearful vs. happy faces. As fearful compared to happy faces are comparatively difficult to detect, as also suggested by our behavioral findings, this activation increase might reflect higher cognitive effort for the recognition of fearful expressions. Neuroimaging studies show IFG involvement in response inhibition in go/no-go tasks (Aron et al., 2004; Logan and Cowan, 1984). Especially right IFG activation is therefore believed to indicate the suppression of response tendencies (Menon et al., 2001; Rubia et al., 2003) and attentional control for the detection of

important cues (Hampshire et al., 2010). Moreover, evidence suggests that the right IFG processes emotional communicative signals in facial expression of others (Nakamura et al., 1999) and that impairment of the IFG is associated with alexithymia (Hobson et al., 2018). Accordingly, these findings indicate that the observed neuronal activity for fearful vs. happy faces primarily reflects an activation increase due to the more difficult detection and evaluation of physical changes in the development of fearful expressions, rather than a stronger fear response as observed in fear conditioning mediated by the amygdala (LeDoux, 2003).

4.2. Context-sensitive emotional inference and connections to interoceptive sensibility and accuracy

Another part of our results confirmed our hypothesis that the subjective individual evaluation of the ability to perceive body signals (*interoceptive sensibility*, IS) is associated with a more precise adaptation of emotional predictions. In line with the results observed in Hübner et al. (2021), RTs of individuals with higher IS decreased with increasing predictability of emotions, i.e., lower entropy of an emotion occurrence, whereas low IS individuals showed the opposite effects, namely decreased RTs to unpredictable emotion. These findings suggest that higher IS individuals benefited from the implemented probabilistic context more than individuals with lower IS. We attribute these results to stronger attentional precision-weighting of individuals with higher IS, which might lead them to learn better from biased probabilities of emotional expressions and thus build stronger expectations (Ainley et al., 2016; Hübner et al., 2021). Correspondingly, using EEG recordings, studies show that interoceptive attention increases cortical processing of heartbeats (Petzschner et al., 2019) and attention independent of emotion processing accelerates the processing of prediction errors (Jiang et al., 2013). Valence-specific affective predictions of expected or unexpected facial expressions have been shown to reduce or enhance cortical responses respectively to interoceptive signals as a function of the probability of repetition (Gentsch et al., 2019). Moreover, when subjects' attention was tuned to their bodily signals by using a HDT, their following conditioned responding was found to be facilitated (Raes and De Raedt, 2011), and individuals with higher IAcc are better in predicting shocks (Katkin et al., 2001).

However, the question remains why interindividual differences in IS and not IAcc were associated with a faster recognition of predicted emotions and to hesitation when unexpected emotions occurred. The MAIA-2 dimensions are constructed as elements of conscious processes of interoception, accessible to self-report (Mehling et al., 2012). Thereby, the MAIA-2 focuses on different regulatory aspects of interoception, i.e., the tendency to ignore or distract oneself from perceived sensations, the ability to sustain and control attention to body sensation and even the ability to regulate psychological distress by attention to body sensations (Mehling et al., 2018). Accordingly, high values in IS represent the perceived awareness of emotional states, but also how easily attention to these sensations can be weighted, sustained or regulated, which involves the adaptation of one's internal states to varying emotional contexts. The assessment of IAcc through the HDT provides a quantification for the objective ability of accurately detecting interoceptive signals (i.e., the heartbeat) in a specified period of time. This is not necessarily related to the regulation of bodily sensations by generating predictions about interoceptive signals, thereby minimizing prediction errors (e.g., Garfinkel et al., 2016). Although this is rather speculative, individuals with high IAcc might therefore tend to show stronger prediction error signals, whereas individuals with high IS (as measured in the present study) weight predictions more strongly. In our paradigm, to regulate attention towards interoceptive changes might be the key ability to raise the precision of interoceptive predictions. Thus, particularly higher IS might result in more frequent and more precisely updated interoceptive predictions.

Regarding the probabilistic context adaptation on the neural level, we rather expected more surprising and less predictable emotions to ac-

tivate regions involved in the signaling of interoceptive prediction errors i.e., AIC, ACC, hippocampus or caudate nucleus (Ahlheim et al., 2014; Bechara et al., 2000; Herry et al., 2007; Schiffer et al., 2012; Seth, 2013b; Strange et al., 2005). However, for more surprising expressions only a single activation in the left postcentral gyrus increased, presumably reflecting simply a more abrupt lifting of the response finger in reaction to more surprising stimuli.

Instead, we found significantly increased activation for more predictable events (*negative entropy*) with a bilateral activity pattern comprising the IFG, posterior insula and middle temporal gyrus. In general, such prediction enhancement effects are proposed to reflect increased activation of predicted elements (Press et al., 2020; Press and Yon, 2019). Interoceptive processing in the insula is proposed to involve posterior-to-anterior regions, with posterior regions supporting primary objective physical features of interoceptive information, whereas the AIC serves the subjective integration of interoceptive and motivational signals (Craig, 2009; Gu et al., 2013; Seth, 2013b, 2012). For example, the processing of cool temperatures was associated with activation in the posterior insula, while subjective ratings of these stimuli were processed in the AIC (Craig et al., 2000). Moreover, the latter region has been suggested to respond to interoceptive prediction errors (Paulus and Stein, 2006; Singer et al., 2009), which is why we expected AIC rather for *positive entropy*, i.e., decreased predictability.

Our results support the presented theoretical assumptions, revealing an activation increase for more predictable emotional stimuli exclusively in the posterior part of the insula. As this area is proposed to provide primary interoceptive representation of the physiological condition of the body, it can be derived that if an emotional valence in facial expression of others is perceived over several trials (i.e., accompanied by increased predictability), physiological representations of the body are created and retained. Thus, these physiological representations could lead to higher activity in the corresponding areas (i.e., the posterior insula) and, moreover, influence the perception of subsequent information by interoceptive predictions. In accordance, we observed increased IFG activation for more predictable facial expressions. Previous research showed increased stimulus-evoked activity in the right IFG and right temporal-parietal junction to be associated with better performance on the next trial, suggesting these regions to be involved in stimulus-triggered reorienting of attention toward behaviorally relevant stimuli (Craig, 2009; Weissman et al., 2006). These findings are consistent with our behavioral results and our assumption that the ability to sustain and control attention towards interoceptive changes might be crucial to raise the precision of interoceptive predictions.

4.3. Interoceptive abilities and their neuronal representations

Finally, we aimed to test more specifically whether the extent of activation increase in brain regions subserving interoceptive processing, i.e., insula and ACC, positively correlates with IS or IAcc. For the parametric effects of entropy and surprise we further included the caudate nucleus as a ROI, as this area was often reported for perceptual prediction errors (Schiffer and Schubotz, 2011; Schiffer et al., 2012). We expected individuals with higher IS or IAcc to build stronger interoceptive predictions and hence show increased activation for more surprising and less predictable events in regions which process perceptual or interoceptive prediction errors. Indeed, the individual IAcc score was positively correlated with the caudate response to entropy and surprise, and with the insula response to entropy. Hence, there was a higher BOLD activation in these regions for the occurrence of less predictable or more surprising events, or both, in individuals with higher vs. lower IAcc scores. No such correlations were observed for the IS.

Imaging studies found significant activation of the insula, ACC and IFG during different variations of the HDT (see Schulz, 2016 for a meta-analysis). Interoceptive attention has been associated with increased AIC activation (Chong et al., 2017; Wang et al., 2019) and interoceptive awareness was shown to change intra-insula signal flows

(Kuehn et al., 2016). Moreover, IAcc has been found to positively covary with activation in the insula cortex, cingulate gyrus and somatosensory cortex (Critchley et al., 2004; Pollatos et al., 2007; Wang et al., 2019).

In contrast, individual IS scores did not correlate with beta estimates of ACC, insula or caudate nucleus. Indeed, little is known about brain areas that may reflect individual IS traits. Recently, Smith et al. (2021) could not find any correlation between the functional connectivity of the insula with individuals' MAIA scores, and hence suggested that brain areas reflecting the individual IS score show only minor overlap with regions reflecting the individual IAcc score. Moreover, Wang et al. (2020) even found a higher IS to be associated with decreased connectivity of AIC and ACC to temporal and frontal regions. These findings are also consistent with our results indicating that higher IAcc, but not IS, positively correlates with activation in brain regions processing perceptual and interoceptive prediction errors, i.e., insula and caudate nucleus. Since the behavioral effects related to the recognition of different emotional valences and the adaptation of emotional predictions differed between IS and IAcc, it is not surprising that different brain regions are also associated with the individual IS and IAcc values. A stronger relationship between IAcc and AIC and striatal activation might indicate stronger processing of interoceptive prediction errors in highly IAcc individuals. Higher IS might rather be associated with the ability to regulate attention to, i.e., generating predictions about interoceptive changes, which might be processed, *inter alia*, in the posterior insula and the IFG (as the posterior insula provides the primary interoceptive representation of the body's physiological state and the IFG is involved in reorienting of attention toward relevant stimuli, see Section 4.2). These assumptions still need to be investigated in further studies in which differences between IS and IAcc can also be statistically tested. This would require combining subjective and objective measures in one task, for example by scoring the subjective confidence in interoceptive accuracy to quantify IS (Garfinkel et al., 2015). Here, it may also be of interest to investigate whether IAcc and IS scores are related to resting state networks (e.g., Salamone et al., 2021). Nevertheless, our study is the first to provide new insights and direct empirical investigations of the different interoceptive facets, their impact on interoceptive predictions and neuronal representations.

Finally, it is important to mention that continuous precision optimization and the ability to sustain and control attention to interoceptive changes in individuals with higher interoceptive abilities may not always be an advantage for interoceptive and emotional processes. For example, this can be observed in individuals with anxiety disorders, which promote increased attention to body signals (Domschke et al., 2010). On the contrary, low interoception has been shown to be accompanied by alexithymia, i.e., deficits in identification and description of one's own and others' emotions (Brewer et al., 2016; Herbert et al., 2011).

4.4. Limitations

The heartbeat detection task (HDT; Schandry, 1981) has emerged as a widely used method for an objective assessment of IAcc (Khalsa et al., 2009; Pollatos and Schandry, 2004) and was used in this study to ensure comparability with thematically related studies on IAcc (e.g., Terasawa et al., 2014). Nevertheless, the method has been increasingly criticized in recent studies (see Coll et al., 2021 for a meta-analysis), since several non-interoceptive processes have been shown to significantly affect the results obtained with the HDT (Desmedt et al., 2018; Murphy et al., 2018; Zamariola et al., 2018). Accordingly, future studies might benefit from either including different or repeated HDT tasks (Wittkamp et al., 2018), including a version with adapted task instructions (Corneille et al., 2020; Desmedt et al., 2020, 2018) or considering other interoceptive tasks that focus on the detection of bodily signals outside of the cardiac domain (e.g., Van Den Houte et al., 2021). Furthermore, since recent studies suggest that HDT results are also biased by alterations in higher-order cognitive domains, future studies may benefit

from considering interoceptive tasks that rely less on cognitive processes (e.g., Fittipaldi et al., 2020; Salamone et al., 2020).

5. Conclusion

Our results provide new insights into how interoceptive accuracy and sensibility shape emotion recognition and interoceptive predictions at the behavioral and the brain level. In particular, individuals with higher interoceptive sensibility were found to show a more precise adaptation to biased probabilities of emotion. Moreover, BOLD effects suggest a different neural basis of interoceptive accuracy and sensibility. Future studies can build on these results and expand knowledge about different interoceptive abilities and their neural implementations, e.g., to provide a basis for the diagnosis and treatment of psychiatric disorders based on interoception deficits.

Data Availability

All relevant data are within the paper and its Supporting information files. For reasons of transparency, additional files are publicly available under the following link: <https://osf.io/z244eg/>

Credit authorship contribution statement

Amelie M. Hübner: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft. **Ima Trempler:** Conceptualization, Formal analysis, Methodology, Software, Writing – review & editing. **Ricarda I. Schubotz:** Conceptualization, Project administration, Resources, Supervision, Writing – review & editing.

Acknowledgement

We sincerely thank Monika Mertens for the assistance in data acquisition. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.neuroimage.2022.119524](https://doi.org/10.1016/j.neuroimage.2022.119524).

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