Contents lists available at ScienceDirect





Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Interoceptive awareness mitigates deficits in emotional prosody recognition in Autism



James S. Mulcahy^{a,b,*}, Matthew Davies^b, Lisa Quadt^{a,b}, Hugo D. Critchley^{a,b,c,d}, Sarah N. Garfinkel^{a,b,c,d}

^a Psychiatry, Brighton and Sussex Medical School, Falmer, BN1 9RR, UK

^b Neuroscience, Brighton and Sussex Medical School, BN1 9RR, UK

^c Sackler Centre for Consciousness Science, University of Sussex, Falmer, BN1 9RR, UK

 $^{\rm d}\, {\it Sussex}$ Partnership NHS Foundation Trust, Brighton, BN2 3EW, UK

ARTICLE INFO

Keywords: Autism Autonomic Emotion Empathy Interoception Metacognition

ABSTRACT

The sensing of internal bodily signals, a process known as interoception, contributes to subjective emotional feeling states that can guide empathic understanding of the emotions of others. Individuals with Autism Spectrum Conditions (ASC) typically show an attenuated intuitive capacity to recognise and interpret other peoples' emotional signals. Here we test directly if differences in interoceptive processing relate to the ability to perceive emotional signals from the intonation of speech (affective prosody) in ASC adults. We employed a novel prosody paradigm to compare emotional prosody recognition in ASC individuals and a group of neurotypical controls. Then, in a larger group of ASC individuals, we tested how recognition of affective prosody related to objective, subjective and metacognitive (awareness) psychological dimensions of interoception. ASC individuals showed reduced recognition of affective prosody compared to controls. Deficits in performance on the prosody task were mitigated by greater interoceptive awareness, so that ASC individuals were better able to judge the prosodic emotion if they had better insight into their own interoceptive abilities. This data links the ability to access interoceptive representations consciously to the recognition of emotional expression in others, suggesting a crossmodal target for interventions to enhance interpersonal skills.

1. Introduction

Emotions fall into categories that are broadly differentiable by their affective and motivational flavour and by their individual behavioural response repertoires. These are underpinned by patterned changes in both central neural responses and peripheral bodily physiology (Kreibig, 2010; Tracy & Randles, 2011). Affective and physiological representations undergo higher contextual and retrospective appraisal, from which the specific emotional experience is ultimately constructed (Barrett, 2017; Seth, Suzuki, & Critchley, 2011). Importantly, it has been argued that the sensing of changes in bodily physiology shape and inform subjective emotional feeling states (Lange, James, & Dunlap, 1967).

Interoception encompasses the afferent signalling, central processing, neural and mental representation of internal (visceral) bodily signals (Critchley & Garfinkel, 2017). Interoception can be partitioned according to channel (e.g. humoral or neural; spinothalamic/vagal) and organ (e.g. cardiac, vascular, gastrointestinal). Moreover, at the psychological level, interoception can be parsed into dissociable objective, subjective and metacognitive dimensions (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Objective measures of 'interoceptive accuracy' can be derived from performance on behavioural tests of interoception (e.g. tests of heartbeat perception). Subjective interoception, 'interoceptive sensibility', reflects self-reported measures of interoceptive experience, which can be quantified using questionnaires. Metacognitive interoception, 'interoceptive awareness', refers to the level of insight of individuals into their own interoceptive performance. This can be computed from the correspondence between objective and subjective interoceptive measures (e.g. trial-by-trial judgments of task performance accuracy and confidence). Across normative populations, these dimensions are dissociable (Garfinkel et al., 2015). Relationships are reported between heightened interoceptive accuracy and the intensity of subjective emotional experiences (Pollatos, Traut-Mattausch, Schroeder, & Schandry, 2007; Wiens, Mezzacappa, & Katkin, 2000). Moreover, the mismatch between subjective / objective and the related metacognitive aspects of

https://doi.org/10.1016/j.biopsycho.2019.05.011 Received 28 June 2018; Received in revised form 4 April 2019; Accepted 31 May 2019

Available online 01 June 2019 0301-0511/ © 2019 Elsevier B.V. All rights reserved.

^{*} Corresponding author at: The Trafford Centre, Psychiatry, Brighton and Sussex Medical School, Falmer, BN1 9RR, UK. *E-mail address*: j.mulcahy@bsms.ac.uk (J.S. Mulcahy).

interoception are implicated clinically in the genesis of psychological symptomatology (Garfinkel, Tiley et al., 2016; Yoris et al., 2015). More broadly, the established relationships between interoceptive processing and emotional experience (e.g. Barrett, Quigley, Bliss-Moreau, & Aronson, 2004; Craig, 2003; Seth, 2013) support the notion that human emotions encompass feeling states that draw upon interoceptive abilities.

Autism Spectrum Conditions (ASC) are a set of pervasive neurodevelopmental syndromes characterised by social and emotional impairments, restrictive, repetitive behaviours, sensory abnormalities and communication difficulties. Particular impairments are described in identifying emotions in self and others (Hill, Berthoz, & Frith, 2004; Hubert et al., 2007). Within the ASC population, explicit deficits in empathy can occur in the presence of empathic bodily responses (Gu et al., 2015), suggesting that ASC individuals have difficulty integrating their intact (or even heightened) physiological responses to emotional cues into overt emotional judgements and subjective empathy. At the neural level, circuits involving the 'viscerosensory' insular cortex support the representation of autonomic and visceral information (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Harrison, Gray, Gianaros, & Critchley, 2010) and, through the anterior insula, conscious access to interoceptive signals and their integration with sensory representations in other modalities. By extension, the insular cortex is considered a critical neural substrate for emotional awareness (Craig, 2009; Critchley et al., 2004; Harrison et al., 2010; Pollatos, Kirsch, & Schandry, 2005; Singer, Critchley, & Preuschoff, 2009; Terasawa, Shibata, Moriguchi, & Umeda, 2012). Insula reactivity is reported to be abnormal in ASC individuals when engaged in processing emotional and motivational information, including; the appraisal of social rewards (Leung, Pang, Anagnostou, & Taylor, 2018); active inhibition of responses to affective stimuli (Duerden et al., 2013); interpretation of bodily expressions (Hadjikhani et al., 2009), and; evaluation of incongruent emotional information (Watanabe et al., 2012). ASC individuals also show alterations in the intrinsic functional connectivity between insular regions and other brain centres involved in emotion and sensory processing (Anteraper et al., 2018; Cheng et al., 2017; Xu et al., 2018). Together, these findings are consistent with the hypothesis that deficits in emotional processing in ASCs may arise, in part, through neurobiological differences in substrates for interoceptive representation, integration, and appraisal.

ASC individuals are reportedly impaired at translating salient interoceptive signals into higher order brain representations (Fiene & Brownlow, 2015; Uddin, 2015). Sensory differences associated with ASC extend to a reported hyposensitivity to interoceptive cues, impairing accurate detection of internal bodily sensations (Elwin, Ek, Schröder, & Kjellin, 2012). ASC individuals also manifest abnormalities in the temporal binding of information across sensory modalities: there is an expansion of audio-visual, visual-tactile and cardio-visual temporal binding windows, referring to the temporal window over which participant's judge two events as occurring in synchrony (Noel, Lytle, Cascio, & Wallace, 2018). This observation is relevant to the interpretation of the heartbeat discrimination task commonly used to quantify interoceptive accuracy from synchrony judgements between heartbeat and external stimuli (Brener & Kluvitse, 1988; Whitehead, Drescher, Heiman, & Blackwell, 1977). The wider temporal binding window of ASC individuals suggests a core difference in higher-order cross-modal sensory integration. Putatively, this difference may specifically compromise emotional flexibility, in part through the sluggish central integration of interoceptive signals with prior affective representations and/or new exteroceptive information. In ASCs, objective interoceptive accuracy can be impaired in both adults (Garfinkel, Tiley et al., 2016; Mul, Stagg, Herbelin, & Aspell, 2018) and children (Palser, Fotopoulou, Pellicano, & Kilner, 2018). However, deficits in heartbeat detection accuracy are not always observed (Nicholson et al., 2018; Schauder, Mash, Bryant, & Cascio, 2015). Variability in interoceptive accuracy reported across studies of ASC may be driven by variation in symptom profiles, e.g. the extent of anxiety or, notably, the presence or absence of alexithymia (Shah, Hall, Catmur, & Bird, 2016).

Simulation of neural and bodily states may underpin and facilitate the recognition of (and empathy for) emotional states of other individuals (Gallese & Goldman, 1998; Jackson, Meltzoff, & Decety, 2005; Lee, Dolan, & Critchley, 2008; Singer et al., 2009). There is evidence within the visual domain for interoceptive facilitation of emotional judgements, e.g. from facial expressions (Garfinkel et al., 2014; Gray et al., 2012). However, in the auditory domain, the relationship between interoception and the discrimination of emotional intonation of speech (affective prosody) is underexplored. Affective prosody refers to the use of non-linguistic features of speech, for example varied pitch and volume, to convey emotional information in support of adaptive interpersonal communication and social exchange (Hubbard, Faso, Assmann, & Sasson, 2017; Shriberg et al., 2001). Affective prosody is distinct from pragmatic prosody, defined as the accenting of words or syllables to convey meaning, and syntactic prosody, which refers to the use of boundary markers or pauses or the segmentation of utterances (Peppé, Cleland, Gibbon, O'Hare, & Castilla, 2011).

ASC individuals can manifest marked deficits in the production and recognition of affective prosody. This is consistent with other emotional processing deficits commonly associated with ASCs (Hadjikhani et al., 2009; Hill et al., 2004). Possible basic mechanisms that have been proposed to underlie these deficits include altered perceptual processing (Adolphs, Sears, & Piven, 2001; Williams, Goldstein, & Minshew, 2006), impaired multimodal sensory integration (Lerner, McPartland, & Morris, 2013), impaired integration of perceptual information and social contextual information (Mottron, Dawson, Soulieres, Hubert, & Burack, 2006), dysfunctional mirror neuron system (Dapretto et al., 2006), atypical gaze and attention toward facially expressed emotions (Black et al., 2017), and impaired theory of mind (Baron-Cohen, 1997). Aberrant interoception may also provide a plausible account extending evidence for impaired sensory integration in ASC to the interoceptive (rather than exteroceptive) domain. Individuals with ASC may be impaired in sensing and integrating the affective information contained within their own bodily responses when inferring the emotions of others. The recognition of emotional prosody may thus rely on such interoceptive reference.

Affective prosodic information is important to smooth social interaction (Wang & Tsao, 2015). For many individuals with ASC, prosodic impairment may exacerbate awkward social communication. However, difficulties in processing affective prosody vary across ASC individuals. Correspondingly, some studies report marked impairments (Golan, Baron-Cohen, & Hill, 2006; Lindner & Rosén, 2006; Peppé et al., 2011; Rosenblau, Kliemann, Dziobek, & Heekeren, 2017), while others fail to show significant differences between ASC individuals and controls (Brennand, Schepman, & Rodway, 2011; Grossman, Bemis, Skwerer, & Tager-Flusberg, 2010; Le Sourn-Bissaoui, Aguert, Girard, Chevreuil, & Laval, 2013). Male-female differences may contribute to some of this variability; observed gender specific dissociation (e.g. Rosenblau et al., 2017; Schneider et al., 2013), is not always replicated (e.g. Hubbard et al., 2017; McLennan, Lord, & Schopler, 1993; Rivet & Matson, 2011). Other factors that may further account for this inconsistency include small group size, methodological differences, wide variance in

performance and study-particular features of research participants. We also hypothesize that individual differences in interoception may be an important contributing factor, wherein deficits in interpreting affective prosody may be amplified when coupled to aberrant interoceptive processing.

Here, based on the notion that the sensing and representation of interoceptive bodily signals underpins emotional feeling states, and hence the capacity to understand emotional information in self and others, we investigated the relationship between affective prosody recognition and interoceptive abilities in ASC individuals. We hypothesized that ASC adults, relative to neurotypical controls, would show reduced performance on a test of prosodic emotional discrimination. Moreover, within a larger group of ASC adults, we hypothesized that reduced prosodic accuracy would correspond with reductions in both interoceptive accuracy and metacognitive interoceptive awareness.

2. Method

2.1. Participants

74 participants with a confirmed ASC diagnosis (38 male, 36 female; mean age 36.7; range 18–64 yrs) and 20 neurotypical controls (9 male, 11 female, mean age 34; range 22–51 yrs) took part in the study. 20 participants from the ASC group (mean age = 34.95, range 20–57 yrs) were age and sex matched to controls, with equal numbers of males and females in each group, to allow for a direct comparison between groups. All ASC participants were fluent English speakers, 6 were left handed and the remaining 68 were right handed. None of the ASC

2.2. Materials and procedure

2.2.1. Prosody paradigm

The affective prosody protocol was designed using Paradigm Experiments software (2016). All emotions were taken from the EU Emotion stimulus set (O'Reilly et al., 2012) which comprises 507 audio files and 166 photographs depicting 21 different emotions. The stimulus set features a diverse balance of adults and children of both genders and various races. All photographs and audio files have been validated in three languages to confirm they represent their assigned emotional labels (O'Reilly et al., 2016). Emotions included feature the six basic emotions; happy, sad, disgusted, surprised, angry, afraid (Ekman, 1992). These were presented in two levels of intensity - regular and mild. In addition, thirteen complex emotions were also included; bored, kind, jealous, unfriendly, hurt, disappointed, interested, joking, ashamed, proud, excited, frustrated and worried. The audio clips were content neutral to ensure that emotion may only be detected through prosodic cues. Any audio clips deemed to include semantic content were removed and omitted from the study.

Three different trial types were utilised; matching voices to faces (face-only), matching voices to emotion descriptors (text-only) and matching voices to faces and emotion descriptors combined (face with text) (Fig. 1). Each domain was further divided into positive and negative valence. In total 114 trials were completed (38 face-only, 38, text-only and 38 face with text). Each of the 19 verbally expressed emotions were presented twice for each domain but remained novel. The presentations were randomised and no trials were repeated. Out of 114 trials, 72 were of a negative valence (24 out of each trial type).



Fig. 1. Stimuli examples - face-only (A), text-only (B) and face with text (C). Each trial displayed one stimulus type with four different emotion choices.

participants had a history of past head injury or organic brain disorders, cognitive impairment or a learning disability (general mental impairment); none had asthma/respiratory illnesses, epilepsy or evidence of psychotic experiences. 10 ASC participants reported that they had completed GCSE's or similar, 16 A level or similar, 13 attended university or business college but did not receive a degree, 23 had received an undergraduate degree and 12 had received a postgraduate degree.

Control participants were recruited from the University of Sussex and members of the local community. ASC participants were recruited from the Sussex Partnership Neurobehavioral Clinic as well as through advertisements placed on social media and via leaflets and posters. All participants provided written informed consent with all procedures approved by the local ethics committee at the University of Sussex, School of Psychology, and the NHS Research Ethics Committee.

Participants were first instructed to put on over-the-ear headphones and were presented with on screen instructions explaining that they would hear audio clips of different phrases and that they should "focus on the tone of voice as much as possible". After each audio clip, they were presented with different emotion options in the form of facial expressions (Fig. 2A, face only condition), words (Fig. 2B, text only condition) or faces with words (Fig. 2C, face/text combined condition). Their task was to decide which of the emotions best matched the tone of voice in the clip that they had just heard. Once it was clear that participants fully understood the task, they then progressed to the main experiment. This comprised 114 trials, where the voice was played while the four different emotion options were presented simultaneously on the screen (Fig. 2). Depending on trial type, these were either in the form of face only, text only or face/text combined, all four options remained on screen until the user responded. The dependant variable was response accuracy, measured as the correct selection of the matching emotion.



A

SAD	PROUD
INTERESTED	НАРРҮ





Fig. 2. Example baseline trials of face only (A), text only (B) and face/text combined (C) stimuli.

2.2.2. Interoceptive accuracy

Two measures were used to determine objective behavioural interoceptive accuracy in the ASC group: the heartbeat-tracking task (Schandry, 1981) and the heartbeat discrimination task (Katkin, Reed, & Deroo, 1983; Whitehead et al., 1977). Participants' heartbeat was measured at rest using a medical-grade pulse oximeter (Nonin4600 pulse oximeter, Nonin Medical Inc. Plymouth MN USA) fitted with soft finger cuff (not tension / spring-loaded). Importantly, the output of the pulse oximeter was available as a waveform (75 Hz sample rate) for accurate timing of tones on the discrimination task.

Participants first completed the heartbeat-tracking task, and were required to concentrate on their heartbeat and without physically checking, silently count how many heartbeats they felt in their body from the time they heard "start" to when they heard "stop". Six durations, presented in a random order, of 25, 30, 35, 40, 45 and 50 s were used. After each trial, participants completed a visual analogue scale (VAS), with a scale of 0–10, to signal confidence of their decision.

Previous research has demonstrated a positive relationship between heartbeat-tracking performance accuracy with IQ (Mash, Schauder, Cochran, Park, & Cascio, 2017; Murphy et al., 2018). Although years of education and educational attainment provide a pragmatic measure for general intelligence, only a subset of our participants had formal IQ measures (N = 39). We therefore did not enter performance on the heartbeat-tracking task into further analyses. Consequently, the present study focused on results obtained from the heartbeat discrimination test.

The heartbeat discrimination task involved the presentation of a periodic external stimulus and participants were tasked with identifying whether the tones were presented synchronous or asynchronous with their own heartbeat. Participants were presented with 10 auditory tones, 20 times to form 20 trials. Tones were presented at 440 Hz with a 100 ms duration. In the heartbeat discrimination task, tones were triggered at the rising edge of the pulse pressure wave, representing mid ventricular systole, on synchronous trials. On the delayed trials, tones were triggered 300 ms after the rise of the pulse pressure wave, representing early diastole. Adjusting for an average pulse transit time of 250 ms, these tone timings corresponded to 250 ms or 550 ms after the ECG R-wave, putatively the time of peak perceptual differentiation. At the end of each trial, participants reported whether the tone was synchronous or asynchronous with their heartbeats, and then provided a confidence rating using the VAS scale. The auditory tones were always presented at the participant's own heart rate, hence the participant was unable to use the tempo of tones or knowledge about their own heart rate to inform their response (Garfinkel et al., 2015).

2.2.3. Interoceptive sensibility

All participants in the ASC group completed the awareness section of the Porges Body Perception Questionnaire (Porges, 1993). The scale comprises of 45 questions pertaining to bodily sensations and participants indicate their awareness of each sensation using a five-point scale ranging from 'never' to 'always'. ASC participants also completed the Multidimensional Assessment of Interoceptive Awareness (MAIA) (Mehling et al., 2012). Confidence judgments were also taken after each trial in both the heartbeat tracking and heartbeat discrimination tasks to determine confidence in task performance accuracy.



Fig. 3. Mean prosodic accuracy scores in the ASC and control groups across each trial type; face, face with text, and text. A main effect of group signified that the ASC group was impaired for all types of stimuli and the main effect of trial type revealed all participants performed worse on face vs text trials and face vs face with text trials. * Significant at the 0.05 level, ** significant at the 0.01 level.

2.2.4. Interoceptive awareness

Interoceptive awareness, also termed interoceptive insight (Khalsa et al., 2018) and interoceptive metacognition (Garfinkel, Manassei et al., 2016) is a metacognitive measure derived from confidence-accuracy correspondence (Garfinkel et al., 2015). For the discrimination task, interoceptive awareness was quantified using receiver operating characteristics (ROC) curve analysis (Green & Swets, 1988) for confidence-accuracy correspondence. ROC analysis indexes the strength of correspondence between confidence (measured by VAS) and a binary state variable, i.e. correct or incorrect asynchrony judgements during heartbeat discrimination. Confidence judgements were divided by hit rate, the proportion of correct trials on which confidence was high, and the false alarm rate, the proportion of incorrect trials on which confidence was high. The ROC curve then gives a measure of the extent to which confidence reflects accuracy, independent of the participant's propensity to report high confidence (Garfinkel et al., 2015).

2.2.5. Questionnaires

In addition to completing the awareness sub-scale of the BPQ and the MAIA, participants in the ASC group also completed the Autism Quotient (AQ) (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), the State-Trait Anxiety Inventory (STAI) (Spielberger, Gorsuch, & Lushene, 1970), the Patient Health Questionnaire (PHQ-9) (Kroenke, Spitzer, & Williams, 2001) and the Toronto Alexithymia Scale (TAS-20) (Bagby, Parker, & Taylor, 1994). Participants in the control group completed the AQ and the STAI. For each questionnaire, the total score was computed and used in the analysis. For the MAIA, each sub-scale was scored as the average score of each question included in that category.

2.3. Data analysis

Group differences in age, anxiety and AQ scores were determined using independent sample t-tests. Between-group differences in performance of the prosody task were assessed using a 2 × 3 ANOVA with group as the between-subjects factor (ASC, control) and trial type as the within-subject factor (face, face with text, text). We also tested for effects of emotional valence and emotional complexity by conducting 2 mixed 2 × 2 × 3 ANOVAs with group as the between-subjects factor (ASC, control) and trial type (face, face with text, text) and emotion (positive vs negative / basic vs complex) as within-subject factors. State and trait anxiety were subsequently entered as separate covariates to check that group differences could not be ascribed to individual differences in anxiety symptomatology. The relationship between interoception and prosody was investigated in the larger ASC sample (N = 74) by separately entering the three dimensions of interoception, accuracy, sensibility and awareness, as covariates into a one-way ANCOVA, with trial type as the within-subject factor. A separate ANCOVA was run on each sub-scale of the MAIA. We also examined the effect of emotional valence and emotional complexity by conducting 2, 2×3 ANCOVAs (with emotion – positive vs negative / complex vs basic, and trial type as within-subject factors) and subsequently entering the three dimensions of interoception as covariates. Significant effects pertaining to interoceptive awareness and emotional prosody were followed up with correlational analyses to explore the effects of sex. The significant differential relationship between interoceptive awareness and prosody accuracy in males versus females was ascertained by computing a Fisher's r to z transformation so z scores could be compared and analysed for statistical significance (Lenhard & Lenhard, 2014).

Within-group individual differences in prosody performance were examined and AQ scores, TAS-20 scores, trait anxiety and depression scores were added individually to each ANCOVA to understand the relative contribution of ASC, alexithymia and affective symptomatology to prosodic accuracy. Heart rate was controlled for in all ASC analyses not involving the control group by entering mean BPM as a covariate (3 participants had missing BPM data so were not included in these analyses). Significant interactions were further explored using paired sample t-tests and bivariate Pearson's correlations.

To better understand the contribution of interoception to affective prosody recognition, and to demonstrate the relative contribution of each variable while controlling for the influence of the other factors, a multiple regression analysis was performed. Interoceptive accuracy and awareness scores, mean BPM, average confidence ratings, AQ scores, STAI (trait), TAS-20 scores, age, sex and the interaction between sex and interoceptive awareness were entered as predictor variables.

3. Results

3.1. Demographic data

Twenty participants from the ASC group were age (t(38) = 0.244, p = 0.808) and sex matched to neurotypical controls. ASC participants had significantly higher state (mean 45.85; SD 9.6) (t(37) = -2.843, p = 0.007) and trait (mean 57.1; SD 8.3) (t(37) = -5.080, p < 0.001) anxiety scores compared to controls (mean 36.26; SD 11.42; mean 41.9; SD 10.33 for state and trait respectively). As expected, AQ scores were significantly higher in the ASC group (mean 35.05; SD 6.2) compared to controls (mean 14.65; SD 5.7) (t(38) = -10.825, p < 0.001).

3.2. Prosody accuracy in ASC vs controls

Participants in the ASC group were significantly impaired in affective prosody recognition relative to control participants across all trial types, as signified by a main effect of group (F(1, 38) = 5.283, p = 0.027). Withinsubject effects revealed a main effect of trial type (F(2, 76) = 21.464, p < 0.001) although no interaction effect between trial type and group was observed (F(2, 76) = 0.097, p = 0.784). Thus all participants, irrespective of whether they had an ASC diagnosis, were significantly poorer at matching emotional prosody for face alone stimuli relative to both face with text (t(39) = -6.009, p < 0.001) and text alone (t(39) = -4.762, p < 0.001) (Fig. 3). The main effect of group was maintained when both trait and state anxiety were separately entered as a covariate (F(1, 36) = 7.101, p = 0.011 and F(1, 36) = 5.394, p = 0.026, respectively), indicating that the reduction in prosody performance in the ASC group was not driven by elevated anxiety levels.

There was no main effect of emotional valence (F(1,38) = 0.102, p = 0.751), but emotional valence significantly interacted with trial type (F(2, 76) = 3.738, p = 0.028). Here, negative emotions were recognized significantly better than positive emotions for text trials (t(39) = -2.35, p = 0.024), while no negative emotion advantage was conferred to either



Fig. 4. Relationship between overall prosody accuracy and interoceptive awareness (r = 0.238, p = 0.047) (A). This was driven by a significant relationship between prosody accuracy and interoceptive awareness in (B) males (r = 0.384, p = 0.021), a relationship not seen in (C) females (r = -0.144, p = 0.422). The correlations in males and females differed significantly (p = 0.023).

face trials (t(39) = 0.97, p = 0.34) or face with text trials (t(39) = 0.80, p = 0.80)p = 0.43). A significant main effect of emotion complexity was identified (F(1, 38) = 26.139, p < 0.001) but no interaction effect was observed between emotion and group (F(1, 38) = 0.615, p = 0.438). Thus, regardless of an ASC diagnosis, all participants were significantly poorer at identifying complex emotions compared to basic emotions (t(39) = 5.138), p < 0.001). Emotional complexity also interacted with trial type (F(2, 76)) = 17.670, p < 0.001) indicating all participants were worse at identifying complex emotions on face trials (t(39) = 6.461, p < 0.001) and on text trials (t(39) = 4.360, p < 0.001) but not on face with text trials (t(39) = -0.944, p = 0.351).

3.3. Interoception in ASC: relationship with prosody

Accuracy: We observed no main effect of interoceptive accuracy (F(1, (68) = 2.129, p = 0.149) suggesting interoceptive accuracy did not reliably influence the accuracy with which ASC individuals judged affective prosody. No significant interactions were identified between emotional valence and interoceptive accuracy (F(1. 68) = 1.138, p = 0.290), interoceptive accuracy and trial type (F(2, 136) = 0.663, p = 0.517) or emotional complexity and interoceptive accuracy (F(1, 68) = 3.432, p = 0.068).

Sensibility: Interoceptive sensibility scores, from both the BPQ and the MAIA, revealed no main effect of the BPQ (F(1, 59) = 0.568), p = 0.568) on prosody accuracy. While there was no main effect of MAIA total score (F(1, 54) = 2.123, p = 0.151), significant main effects of the noticing sub-scale (F(1, 54) = 9.138, p = 0.004) and the attention regulation sub scale (F(1, 54) = 4.909, p = 0.031) were observed. No significant interactions were identified between emotional valence, emotional complexity, trial type and interoceptive sensibility. There was no main effect of average confidence and all interactions also did not meet threshold significance.

Awareness: Interoceptive awareness scores revealed a main effect of metacognitive interoceptive awareness on the discrimination task (F (1,68) = 4.077, p = 0.047) suggesting prosodic accuracy varied as a function of interoceptive awareness. This relationship between overall prosody accuracy and interoceptive awareness was significant in the overall sample (r = 0.238, p = 0.047) (Fig. 4A) and in males (r = 0.384, p = 0.021) (Fig. 4B), but not females (r = -0.144, p = 0.422) (Fig. 4C). The correlations in males and females differed significantly (p = 0.023).

Interoceptive awareness did not significantly interact with emotional valence (F(1, 68) = 0.450, p = 0.505), emotional complexity (F(1, 68) = 0.450, p = 0.505)(68) = 0.046, p = 0.831) or trial type (F(2, 136) = 0.618, p = 0.540).

3.4. Emotional prosody deficits in ASC: related factors

0.2

0.4

We investigated the relationship between prosody performance and individual differences between ASC individuals. In the extended sample of ASC participants (N = 74), performance did not differ across emotion categories, as reflected by a non-significant effect of emotional valence (F(1, 69) = 0.123, p = 0.727), and a non-significant effect of basic vs complex emotions (F(1, 69) = 1.823, p = 0.181). Accuracy scores significantly differed across trial types (F(2, 69) = 4.072,p = 0.019) indicating ASC participants were significantly worse at identifying prosodic emotion on face vs text (t(73) = -8.380), p < 0.001), face vs face with text (t(73) = -8.541, p < 0.001) but not face with text vs text (t(73) = 1.939, p = 0.056) trials. There was no interaction effect between emotional valence and trial type (F(2, 138) = 0.809, p = 0.447), nor between emotional complexity and trial type (F(2, 138) = 0.346, p = 0.708), suggesting that neither positive vs negative nor basic vs complex emotions provided a consistent recognition advantage across trial types.

AQ: Analysis of AQ scores revealed no significant effect of AQ on prosody accuracy (F(1, 66) = 1.640, p = 0.205) suggesting that prosodic accuracy did not differ as a function of autism severity (as reflected by AQ scores). There were also no interactions between AQ and emotional valence (F(1, 66) = 0.001, p = 0.979), emotional complexity (F(1, 66) = 0.001, p = 0.979)

Table 1

Correlation matrix to demonstrate the relationships between the three psychological dimensions of interoception during heartbeat discrimination and their relationship with affective symptomatology. The first number denotes the r value, the second number denotes the p value.

	Heartbeat discrimination	Awareness	Mean confidence	AQ	Trait anxiety	TAS total	BPQ (awareness section)	Mean BPM
Heartbeat discrimination	1							
Awareness	0.182	1						
	0.120							
Mean confidence	0.375**	0.158	1					
	0.001	0.178						
AQ	0.088	0.192	-0.153	1				
	0.462	0.107	0.201					
Trait anxiety	0.094	0.086	-0.061	0.100	1			
-	0.441	0.482	0.618	0.413				
TAS total	0.150	0.120	-0.092 0.441	0.375**	0.140	1		
	0.206	0.311		0.001	0.251			
BPQ (awareness section)	0.216	0.003	-0.122	0.095	0.346**	-0.063	1	
	0.085	0.982	0.332	0.453	0.006	0.617		
Mean BPM	-0.122	0.204	-0.296*	-0.090	-0.078	0.097	-0.053	1
	0.311	0.088	0.012	0.461	0.532	0.425	0.683	

* Significant at the 0.05 level.

** Significant at the 0.01 level.

66) = 2.586, p = 0.113), or trial type (F(2, 132) = 0.595, p = 0.553).

Alexithymia (TAS-20): No main effect of alexithymia was observed (F(1, 67) = 3.735, p = 0.058). No significant interactions were found between alexithymia and trial type (F(2, 134) = 0.895, p = 0.411), emotional valence (F(1, 67) = 3.203, p = 0.078) or emotional complexity (F(1, 67) = 1.186, p = 0.280).

Affective symptoms (PHQ-9 and STAI_T): No main effect of depression (F(1, 52) = 2.977, p = 0.090) or anxiety (F(1, 63) = 2.141, p = 0.148) was found. No significant interactions were found between depression and emotional valence (F(1, 52) = 2.057, p = 0.157), emotional complexity (F(1, 52) = 0.007, p = 0.932) or trial type (F(2, 104) = 2.540, p = 0.084). There were also no significant interactions between anxiety and emotional valence (F(1, 63) = 2.150, p = 0.081), emotional complexity (F(1, 63) = 3.177, p = 0.079) or trial type (F(2, 126) = 0.804, p = 0.450) See also Table 1 below for a correlation matrix demonstrating the relationship between interoception and affective symptomatology.

3.5. Regression analysis

The regression model was not significant for prosodic accuracy (F (10, 65) = 1.870, p = 0.070, R² = 0.254). However, the contribution of metacognitive interoceptive awareness was the only predictor variable to prevail as significant for the heartbeat discrimination model, p = 0.044, providing evidence of its contribution to affective prosody recognition. A summary of the predictor variables can been seen in Table 2 below.

Table 2

Regression table to demonstrate the relative contribution of each predictor variable to individual differences in prosody accuracy.

Prosody accuracy										
	В	SE B	β	t	р					
AQ	-0.001	0.002	-0.115	-0.821	0.415					
Trait anxiety	0.001	0.001	0.144	1.031	0.307					
Alexithymia	-0.002	0.001	-0.252	-1.922	0.060					
Interoceptive accuracy	0.027	0.081	0.046	0.333	0.740					
Confidence	-0.002	0.005	-0.058	-0.406	0.686					
Interoceptive awareness	0.680	0.329	0.832	2.065	0.044					
Mean BPM	-0.001	0.001	-0.104	-0.664	0.510					
Age	-0.001	0.001	-0.158	-1.048	0.299					
Sex	0.187	0.120	1.061	1.568	0.123					
Sex * Interoceptive awareness	-0.307	0.208	-1.175	-1.481	0.144					

* Significant at the 0.05 level.

4. Discussion

Recognition of emotion from the intonation of speech (affective prosody) was significantly impaired in ASC participants, compared to neurotypical controls, as demonstrated by reduced performance accuracy on a novel prosody paradigm. In a larger ASC sample, prosody performance was linked to the degree of metacognitive interoceptive awareness during the heartbeat discrimination task. Thus, those individuals with better interoceptive insight (on this task) had enhanced prosody recognition. This relationship between affective prosody and interoceptive awareness provides a fresh perspective into brain-body interactions in ASC individuals, where the capacity for conscious insight into one's perception of interoceptive signals appears to facilitate the recognition of emotional prosody.

Influential 'peripheral' theories of emotion relate the sensing of internal physiological states of bodily arousal to the emotional experience (Damasio, Everitt, & Bishop, 1996; Lange et al., 1967). Successful cardiac interoception is moreover an important factor in the perception, regulation and expression of emotional information (Critchley & Garfinkel, 2017; Garfinkel et al., 2014). Even low-level afferent signals concerning cardiac arousal (arterial baroreceptor firing with each individual heartbeat) influence the detection and experience of emotional facial expression (Garfinkel et al., 2014). However, the results of the current study did not find a simple and reliable relationship between prosody and objective measures of interoceptive accuracy. In fact, our findings highlight an effect of a higher-level representation of interoceptive state: metacognitive interoceptive awareness.

Metacognitive interoceptive awareness is, unlike interoceptive performance accuracy, an expression of higher-order conscious access to interoceptive signals (Garfinkel et al., 2015). The current findings suggest that understanding emotional information, in the form of emotional prosody, is functionally dependent upon understanding and interpreting one's own physiological state rather than being accurately (but potentially pre-consciously) guided by the physical sensation of interoceptive signals. Notably, other types of emotion processing (e.g. intensity ratings) are directly associated with interoceptive accuracy (Wiens et al., 2000), yet emotional prosody recognition and inference is arguably more complex, incorporating discrete and interacting processing channels, including pitch, volume and duration, which draw upon distinct neural networks (Buchanan et al., 2000). Affective prosody recognition thus aligns with an interoceptive dimension that is more connected to higher-order conscious access of interoceptive information. Our findings within this autistic sample emphasize the need to quantify interoceptive insight to derive mechanistic insight into the processing of socially relevant emotional information conveyed through

speech, which appears to recruit higher level, metacognitive processes.

Interestingly, our results provide evidence to show that the association between interoceptive awareness and prosodic accuracy is most strongly driven by the male participants in our sample. Male/female differences have been a particular topic of investigation in studies of ASC, driven by influential theoretical considerations (Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003; Baron-Cohen, 2009). Sex differences in brain structure may be attenuated in ASC (e.g. Beacher et al., 2012), yet sex differences in brain function, behaviour and symptomatology are recognised (e.g. Lai et al., 2011; Rivet & Matson, 2011): for example, females show relative preservation in their perception and understanding of emotional information both behaviourally (McGillivray & Evert, 2018) and at the neural level (Schneider et al., 2013; Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008). Indeed, even in healthy populations, females report greater attention to bodily sensations yet actually perform worse than males on the heartbeat-counting task (Grabauskaitė, Baranauskas, & Griškova-Bulanova, 2017). It should be noted, however, that the effects of sex were not significant in the main regression analysis linking effective prosody and interoceptive awareness, presumably due to shared variance with other factors. Thus, our results provide tentative evidence that males may require greater conscious awareness of their internal bodily sensations in order to comprehend affective prosody.

To date, research on the psychology of interoception has focused either on subjective reports (indexed by questionnaires) or on more objective behavioural measures, e.g. performance accuracy during the heartbeat detection task. Historically, the term awareness was used to refer to both subjective and objective measures of interoceptive sensitivity. However, drawing on advances in the cognitive psychology of consciousness awareness, recent terminology equates awareness to metacognition. Correspondingly, there is a paucity of research referring to metacognitive aspects of interoception (e.g. Canales-Johnson et al., 2015; Ewing et al., 2017; Khalsa et al., 2008), and its relative contribution to emotional processing is not fully explored. The mechanisms required to appraise one's own internal bodily sensations may be fundamental to the understanding of emotional information in self and others (Singer et al., 2009). This builds upon previous work that highlights the role of more automatic measures, such as physiological resonance and contagion (Cooper et al., 2014; Harrison, Wilson, & Critchley, 2007; Konvalinka et al., 2011). As the state of others can be mirrored in the observer, interoceptive insight into one's own bodily signals can also shape understanding of the state of others. Correspondingly, people with alexithymia (an inability to perceive and describe one's own emotions), are also impaired in the perception and recognition of emotional expressions (Lane et al., 1996; Parker, Taylor, & Bagby, 1993; Prkachin, Casey, & Prkachin, 2009). Thus, the capacity to understand one's own emotions facilitates the accurate perception of emotion in others. Neuroimaging findings also indicate a sharing of neural architecture during both personal experience of emotion and judging the emotions of others. In particular, the insula, a key structure involved in interoception and emotional processing, shows increased activation both when observing another person's disgust and when experiencing disgust directly (Wicker et al., 2003). Engagement of insular cortex is characteristic of social emotional processing (Lamm & Singer, 2010), particularly empathy (Jackson et al., 2005; Singer et al., 2009).

Alexithymia is extremely common in ASC, but it is not (when subjectively rated) an obligatory, defining attribute of this diagnosis (Bird et al., 2010; Cook, Brewer, Shah, & Bird, 2013; Shah et al., 2016). Since alexithymia is characterised by an inability to identify and describe emotions, the relative contribution of alexithymia to prosodic impairment was also investigated in this study. While we observed a correlation between AQ scores and TAS-20 scores conforming a relationship between ASC and alexithymia (Shah et al., 2016), we saw no reliable relationship between reported levels of alexithymia and affective prosody recognition. Thus, impaired prosodic accuracy in ASC individuals appears to be driven by interoceptive metacognition, and not alexithymia. This represents a potential avenue for intervention, and future work may usefully explore whether individual differences in metacognitive interoceptive awareness predicts sensitivity to emotional prosody in neurotypical populations or if this association is more specific to ASC.

Our finding of impaired emotional prosody recognition adds to literature concerning affective prosody deficits in ASC individuals. We observed a more pronounced impairment on trials that also required face processing. This is perhaps unsurprising, consistent with previously-described difficulties in face processing in ASCs (Dalton et al., 2005; Lynn et al., 2018; Rigby, Stoesz, & Jakobson, 2018). In fact, all participants, irrespective of ASC status, showed a reduced performance on 'face-only' trials, relative to trials with accompanying text that specified the possible emotion.

Previous work has not always demonstrated clear deficits in processing affective prosody in ASC individuals compared to neurotypical controls (Brennand et al., 2011; Golan et al., 2006; Grossman et al., 2010; Le Sourn-Bissaoui et al., 2013; Peppé et al., 2011; Rosenblau et al., 2017), but discrepancies may reflect the varied methodologies employed. Some studies only employed stimuli conveying 'basic' emotions (Globerson, Amir, Kishon-Rabin, & Golan, 2015; Grossman et al., 2010), which are arguably easier to detect (Brennand et al., 2011; Smith, Montagne, Perrett, Gill, & Gallagher, 2010). Other studies vary in the type of stimuli used to assess prosody (Chevallier, Noveck, Happé, & Wilson, 2011; Grossman et al., 2010; Kujala, Lepistö, Nieminen-von Wendt, Näätänen, & Näätänen, 2005; Peppé, McCann, Gibbon, O'Hare, & Rutherford, 2007, 2011) and some studies have used stimuli containing semantic information thus giving emotional information that is non-dependant on prosodic cues (see Wang & Tsao, 2015). The current study accounted for these methodological discrepancies by using semantically-neutral prosodic cues, by combining a range of complex and basic emotions (e.g. Golan et al., 2006) and by employing three different trial types; face only, face with text and text only trials. Our stringent methodology may therefore encourage the use of more robust paradigms to assess the processing of affective prosody.

Notably, we quantified interoceptive dimensions using two different tasks that access both shared and distinct mechanisms (Schulz, 2016), although we focused our examination on only the heartbeat discrimination task. Strong correlations in performance accuracy between these heartbeat-tracking and discrimination tasks are not always observed especially within small samples (Ring & Brener, 2018). The heartbeat tracking task is arguably influenced by prior knowledge about heart rate (Ring, Brener, Knapp, & Mailloux, 2015) and the heartbeat discrimination task requires the integration of interoceptive and exteroceptive information (Garfinkel, Tiley et al., 2016). Recognition of affective prosody may itself be an internal-external integration task, particularly if internal bodily changes elicited by external affective prosody guide correct comprehension and appraisal processes. Indeed, our results suggest a relationship between interoception and prosody, as measured by the cross-modal discrimination task, manifesting in the metacognitive domain only, thus indicative of a higher-level processing deficit.

The observed relationship between prosody and interoceptive awareness highlights the value in investigating interoceptive contributions to adaptive emotional behaviours and clinical symptomatology. Given the impaired recognition of emotional prosody that we observed in ASC individuals, and the role that interoceptive awareness plays in this impairment, targeted interventions aimed at improving interoceptive awareness may be useful to improve emotional processing in this group who are at higher risk of anxiety and mood disorders. Support for this notion lies in the memory domain, wherein better memory performance is associated with a more accurate judgement of one's own performance, a relationship not observable for the interoception tasks (Meessen et al., 2016). One proposed reason of this difference is the availably of feedback: information about the accuracy of memory performance is common in everyday situations, yet feedback about interoceptive performance is not. Therefore, provision of performance feedback during interoceptive tasks, could be used to train ASC individuals to increase interoceptive awareness, and by association to improve emotional prosody recognition. Moreover, individuals who possess good metacognition may be more able to allocate attentional resources to functional domains, e.g. interoception, on which they perform poorly (Schooler et al., 2011). There may thus be synergistic benefits in improving interoceptive metacognition.

There are limitations to the current study that should be addressed in future work. Firstly, the heartbeat discrimination task served as the primary outcome interoceptive measure used. For this task, studies vary in the number of index trials, although it has been claimed that 40–60 trials are needed to ensure robust reliability on this measure of interoceptive performance accuracy (Kleckner, Wormwood, Simmons, Barrett, & Quigley, 2015). Moreover, ROC fit is also enhanced with more trials, and thus this may have also impacted our calculations of interoceptive awareness. Since the task employed here consisted of only 20 trials, this can be considered a limitation. Additionally, due to the design of the prosody paradigm we were unable to examine the effect of interoception on discrete basic emotions, since each basic emotion was only presented 6 times; we were thus underpowered to test this relationship. The absence of a significant relationship between prosodic accuracy and AQ suggests that the prosodic deficits may not be driven by core ASC symptomatology, but instead they may represent a specific feature coupled to aberrant interoceptive processing. However, interoceptive dimensions were not measured within the neurotypical control group. We therefore cannot conclude whether or not the relationship between interoceptive awareness and prosody is specific to autism, nor whether this coupling reflects a core relationship that can be extrapolated to other individuals. Future research should investigate the relationship between prosody and interoception in normative populations to see if the manifestation of prosodic deficits are also driven by reduced interoceptive awareness. Further studies are also needed to test if the interoceptive metacognitive skill required to recognise affective prosody is modality-specific, i.e. does it solely rely on interoceptive awareness, or does the metacognition of knowing when you understand another person's emotions also affect accuracy in labelling emotional cues from speech. Ultimately, a more comprehensive understanding of metacognitive interoceptive awareness is needed to better understand its contribution to emotion and of its presentation in clinical disorders.

The results of the current study provide a novel contribution to understanding affective prosody deficits in ASC individuals, relating low-level processing of social/emotional cues to higher-level appraisal of one's own ability to process physiological changes in one's body. The relationship between interoception and emotions remains pertinent: improved detailed knowledge of their association will enhance insight into the mechanisms underlying core ASC symptomatology and enable targeted strategies to mitigate psychological distress within this population.

Acknowledgments

This work was supported by a grant from MQ: Transforming Mental Health (grant number MQ16PI10016_Critchley) and by the School of Psychology, University of Sussex.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.biopsycho.2019.05.011.

References

Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal processing of social information from faces in autism. Journal of Cognitive Neuroscience, 13(2), 232–240.

- Anteraper, S., Guell, X., D'Mello, A., Joshi, N., Whitfield-Gabrieli, S., & Joshi, G. (2018). Disrupted cerebro-cerebellar intrinsic functional connectivity in young adults with high-functioning autism spectrum disorder: A data-driven, whole-brain, high temporal resolution fMRI study. *Brain Connectivity* (ja).
- 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.
- Baron-Cohen, S. (1997). Mindblindness: An essay on autism and theory of mind. MIT press. Baron-Cohen, S., Richler, J., Bisarya, D., Gurunathan, N., & Wheelwright, S. (2003). The systemizing quotient: An investigation of adults with Asperger syndrome or high-functioning autism, and normal sex differences. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 358*(1430), 361–374.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, malesand females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, 31(1), 5–17.
- Baron-Cohen, S. (2009). Autism: The empathizing–systemizing (E-S) theory. Annals of the New York Academy of Sciences, 1156(1), 68–80.
- Barrett, L. F. (2017). The theory of constructed emotion: An active inference account of interoception and categorization. Social Cognitive and Affective Neuroscience, 12(1), 1–23.
- Barrett, L. F., Quigley, K. S., Bliss-Moreau, E., & Aronson, K. R. (2004). Interoceptive sensitivity and self-reports of emotional experience. *Journal of Personality and Social Psychology*, 87(5), 684.
- Beacher, F. D., Radulescu, E., Minati, L., Baron-Cohen, S., Lombardo, M. V., Lai, M.-C., .. Harrison, N. A. (2012). Sex differences and autism: Brain function during verbal fluency and mental rotation. *PloS One*, 7(6), e38355.
- Bird, G., Silani, G., Brindley, R., White, S., Frith, U., & Singer, T. (2010). Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain, 133*, 1515–1525. https://doi.org/10.1093/brain/awq060.
- Black, M. H., Chen, N. T., Iyer, K. K., Lipp, O. V., Bölte, S., Falkmer, M., ... Girdler, S. (2017). Mechanisms of facial emotion recognition in autism spectrum disorders: Insights from eye tracking and electroencephalography. *Neuroscience and Biobehavioral Reviews*, 80, 488–515.
- Brener, J., & Kluvitse, C. (1988). Heartbeat detection: Judgments of the simultaneity of external stimuli and heartbeats. *Psychophysiology*, 25(5), 554–561.
- Brennand, R., Schepman, A., & Rodway, P. (2011). Vocal emotion perception in pseudosentences by secondary-school children with autism spectrum disorder. *Research in Autism Spectrum Disorders*, 5(4), 1567–1573.
- Buchanan, T. W., Lutz, K., Mirzazade, S., Specht, K., Shah, N. J., Zilles, K., ... Jäncke, L. (2000). Recognition of emotional prosody and verbal components of spoken language: An fMRI study. *Cognitive Brain Research*, 9(3), 227–238.
- Canales-Johnson, A., Silva, C., Huepe, D., Rivera-Rei, Á., Noreika, V., Garcia, M.d. C., ... Sedeño, L. (2015). Auditory feedback differentially modulates behavioral and neural markers of objective and subjective performance when tapping to your heartbeat. *Cerebral Cortex*, 25(11), 4490–4503.
- Cheng, W., Rolls, E. T., Zhang, J., Sheng, W., Ma, L., Wan, L., ... Feng, J. (2017). Functional connectivity decreases in autism in emotion, self, and face circuits identified by Knowledge-based Enrichment Analysis. *Neuroimage*, 148, 169–178.
- Chevallier, C., Noveck, I., Happé, F., & Wilson, D. (2011). What's in a voice? Prosody as a test case for the Theory of Mind account of autism. *Neuropsychologia*, 49(3), 507–517. https://doi.org/10.1016/j.neuropsychologia.2010.11.042.
- Cook, R., Brewer, R., Shah, P., & Bird, G. (2013). Alexithymia, not autism, predicts poor recognition of emotional facial expressions. *Psychological Science*, 24(5), 723–732.
- Cooper, E. A., Garlick, J., Featherstone, E., Voon, V., Singer, T., Critchley, H. D., ... Harrison, N. A. (2014). You turn me cold: Evidence for temperature contagion. *PloS One*, 9(12), e116126.
- Craig, A. D. (2003). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, 13(4), 500–505.
- Craig, A. D. (2009). How do you feel Now? The anterior insula and human awareness. Nature Reviews Neuroscience, 10, 59. https://doi.org/10.1038/nrn2555.
- Critchley, H. D., & Garfinkel, S. N. (2017). Interoception and emotion. Current Opinion in Psychology, 17, 7–14.
- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7(2), 189.
- Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H. H., ... Davidson, R. J. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience*, 8(4), 519.
- Damasio, A. R., Everitt, B. J., & Bishop, D. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philosophical Transactions Biological Sciences*, 351(1346), 1413–1420.
- Ekman, P. (1992). An argument for basic emotions. Cognition & emotion, 6(3-), 169-200.
- Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., ... Iacoboni, M. (2006). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience*, 9(1), 28.
- Duerden, E. G., Taylor, M. J., Soorya, L. V., Wang, T., Fan, J., & Anagnostou, E. (2013). Neural correlates of inhibition of socially relevant stimuli in adults with autism spectrum disorder. *Brain Research*, 1533, 80–90.
- Elwin, M., Ek, L., Schröder, A., & Kjellin, L. (2012). Autobiographical accounts of sensing in asperger syndrome and high-functioning autism. Archives of Psychiatric Nursing, 26(5), 420–429. https://doi.org/10.1016/j.apnu.2011.10.003.
- Ewing, D. L., Manassei, M., Gould van Praag, C., Philippides, A. O., Critchley, H. D., & Garfinkel, S. N. (2017). Sleep and the heart: Interoceptive differences linked to poor experiential sleep quality in anxiety and depression. *Biological Psychology*, 127, 163–172. https://doi.org/10.1016/j.biopsycho.2017.05.011.
- Fiene, L., & Brownlow, C. (2015). Investigating interoception and body awareness in

adults with and without autism spectrum disorder. Autism Research, 8(6), 709–716.
Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. Trends in Cognitive Sciences, 2(12), 493–501.

- Garfinkel, S. N., Manassei, M. F., Hamilton-Fletcher, G., den Bosch, Y. I., Critchley, H. D., & Engels, M. (2016). Interoceptive dimensions across cardiac and respiratory axes. *Philosophical Transactions Biological Sciences*, 371(1708), 20160014.
- Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the heart: Sensitivity to fear stimuli depends on individual heartbeats. *Journal of Neuroscience*, 34(19), 6573–6582.
- 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. https://doi.org/10.1016/j.biopsycho.2014.11.004.
- Garfinkel, S. N., Tiley, C., O'Keeffe, S., Harrison, N. A., Seth, A. K., & Critchley, H. D. (2016). Discrepancies between dimensions of interoception in autism: Implications for emotion and anxiety. *Biological Psychology*, 114, 117–126.
- Globerson, E., Amir, N., Kishon-Rabin, L., & Golan, O. (2015). Prosody recognition in adults with high-functioning autism spectrum disorders: From psychoacoustics to cognition. *Autism Research*, 8(2), 153–163.
- Golan, O., Baron-Cohen, S., & Hill, J. (2006). The Cambridge mindreading (CAM) facevoice battery: Testing complex emotion recognition in adults with and without Asperger syndrome. Journal of Autism and Developmental Disorders, 36(2), 169–183.
- Grabauskaitė, A., Baranauskas, M., & Griškova-Bulanova, I. (2017). Interoception and gender: What aspects should we pay attention to? *Consciousness and Cognition*, 48, 129–137.
- Gray, M. A., Beacher, F. D., Minati, L., Nagai, Y., Kemp, A. H., Harrison, N. A., ... Critchley, H. D. (2012). Emotional appraisal is influenced by cardiac afferent information. *Emotion*, 12(1), 180.
- Green, D. M., & Swets, J. A. (1988). Signal detection theory and psychophysics. Los Altos, CA: Peninsula.
- Grossman, R. B., Bemis, R. H., Skwerer, D. P., & Tager-Flusberg, H. (2010). Lexical and affective prosody in children with high-functioning autism. *Journal of Speech Language and Hearing Research*, 53(3), 778–793.
- Gu, X., Eilam-Stock, T., Zhou, T., Anagnostou, E., Kolevzon, A., Soorya, L., & Fan, J. (2015). Autonomic and brain responses associated with empathy deficits in autism spectrum disorder. *Human Brain Mapping*, 36(9), 3323–3338.
- Hadjikhani, N., Joseph, R. M., Manoach, D. S., Naik, P., Snyder, J., Dominick, K., ... de Gelder, B. (2009). Body expressions of emotion do not trigger fear contagion in autism spectrum disorder. *Social Cognitive and Affective Neuroscience*, 4(1), 70–78. https://doi.org/10.1093/scan/nsn038.
- Harrison, N. A., Gray, M. A., Gianaros, P. J., & Critchley, H. D. (2010). The embodiment of emotional feelings in the brain. *Journal of Neuroscience*, 30(38), 12878–12884.
- Harrison, N. A., Wilson, C. E., & Critchley, H. D. (2007). Processing of observed pupil size modulates perception of sadness and predicts empathy. *Emotion*, 7(4), 724.
- Hill, E., Berthoz, S., & Frith, U. (2004). Brief report: Cognitive processing of own emotions in individuals with autistic Spectrum disorder and in their relatives. *Journal of Autism* and Developmental Disorders, 34(2), 229–235. https://doi.org/10.1023/b;jadd. 0000022613.41399.14.
- Hubbard, D. J., Faso, D. J., Assmann, P. F., & Sasson, N. J. (2017). Production and perception of emotional prosody by adults with autism spectrum disorder. *Autism Research*.
- Hubert, B., Wicker, B., Moore, D. G., Monfardini, E., Duverger, H., Da Fonseca, D., ... Deruelle, C. (2007). Brief report: Recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *Journal of Autism and Developmental Disorders*, 37(7), 1386–1392.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage*, 24(3), 771–779.
- Katkin, E. S., Reed, S. D., & Deroo, C. (1983). A methodological analysis of 3 techniques for the assessment of individual-differences in heartbeat detection. *Psychophysiology*, 20(4) 452–452.
- Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., ... Paulus, M. P. (2018). Interoception and mental health: A roadmap. *Biological Psychiatry Cognitive Neuroscience and Neuroimaging*, 3(6), 501–513. https://doi.org/10.1016/j.bpsc.2017.12.004.
- Khalsa, S. S., Rudrauf, D., Damasio, A. R., Davidson, R. J., Lutz, A., & Tranel, D. (2008). Interoceptive awareness in experienced meditators. *Psychophysiology*, 45(4), 671–677. https://doi.org/10.1111/j.1469-8986.2008.00666.x.
- Kleckner, I. R., Wormwood, J. B., Simmons, W. K., Barrett, L. F., & Quigley, K. S. (2015). Methodological recommendations for a heartbeat detection-based measure of interoceptive sensitivity. *Psychophysiology*, 52(11), 1432–1440.
- Konvalinka, I., Xygalatas, D., Bulbulia, J., Schjødt, U., Jegindø, E.-M., Wallot, S., ... Roepstorff, A. (2011). Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proceedings of the National Academy of Sciences*, 108(20), 8514–8519. https://doi.org/10.1073/pnas.1016955108.
- Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, 84(3), 394–421. https://doi.org/10.1016/j.biopsycho.2010.03.010.
- Kroenke, K., Spitzer, R. L., & Williams, J. B. W. (2001). The PHQ-9: Validity of a brief depression severity measure. *Journal of General Internal Medicine*, 16(9), 606–613. https://doi.org/10.1046/j.1525-1497.2001.016009606.x.
- Kujala, T., Lepistö, T., Nieminen-von Wendt, T., Näätänen, P., & Näätänen, R. (2005). Neurophysiological evidence for cortical discrimination impairment of prosody in Asperger syndrome. *Neuroscience Letters*, 383(3), 260–265.
- Lai, M.-C., Lombardo, M. V., Pasco, G., Ruigrok, A. N., Wheelwright, S. J., Sadek, S. A., ... Consortium, M. A. (2011). A behavioral comparison of male and female adults with high functioning autism spectrum conditions. *PloS One*, 6(6), e20835.

Lamm, C., & Singer, T. (2010). The role of anterior insular cortex in social emotions. Brain

Structure & Function, 214(5-6), 579-591.

- Lane, R. D., Lee, S., Reidel, R., Weldon, V., Kaszniak, A., & Schwartz, G. E. (1996). Impaired verbal and nonverbal emotion recognition in alexithymia. *Psychosomatic Medicine*, 58(3), (1996)).
- Lange, C., James, W., & Dunlap, K. (1967). The emotions (Reprinted). New York: Hafner Publishing Co (1967)).
- Le Sourn-Bissaoui, S., Aguert, M., Girard, P., Chevreuil, C., & Laval, V. (2013). Emotional speech comprehension in children and adolescents with autism spectrum disorders. *Journal of Communication Disorders*, 46(4), 309–320.
- Lee, T.-W., Dolan, R. J., & Critchley, H. D. (2008). Controlling emotional expression: Behavioral and neural correlates of nonimitative emotional responses. *Cerebral Cortex*, 18(1), 104–113. https://doi.org/10.1093/cercor/bhm035.
- Lenhard, W., & Lenhard, A. (2014). Hypothesis tests for comparing correlations. Retrieved fromhttps://www.psychometrica.de/correlation.html.
- Lerner, M. D., McPartland, J. C., & Morris, J. P. (2013). Multimodal emotion processing in autism spectrum disorders: An event-related potential study. *Developmental Cognitive Neuroscience*, 3, 11–21.
- Leung, R. C., Pang, E. W., Anagnostou, E., & Taylor, M. J. (2018). Young adults with autism spectrum disorder show early atypical neural activity during emotional face processing. *Frontiers in Human Neuroscience*, 12, 57. https://doi.org/10.3389/fnhum. 2018.00057.
- Lindner, J. L., & Rosén, L. A. (2006). Decoding of emotion through facial expression, prosody and verbal content in children and adolescents with Asperger's syndrome. *Journal of Autism and Developmental Disorders*, 36(6), 769–777.
- Lynn, A. C., Padmanabhan, A., Simmonds, D., Foran, W., Hallquist, M. N., Luna, B., ... O'Hearn, K. (2018). Functional connectivity differences in autism during face and car recognition: Underconnectivity and atypical age-related changes. *Developmental Science*, 21(1).
- Mash, L. E., Schauder, K. B., Cochran, C., Park, S., & Cascio, C. J. (2017). Associations between interoceptive cognition and age in autism Spectrum disorder and typical development. *Journal of Cognitive Education and Psychology*, 16(1), 23–37.
- McGillivray, J., & Evert, H. (2018). Exploring the effect of gender and age on stress and emotional distress in adults with autism spectrum disorder. *Focus on Autism and Other Developmental Disabilities*, 33(1), 55–64.
- McLennan, J. D., Lord, C., & Schopler, E. (1993). Sex differences in higher functioning people with autism. Journal of Autism and Developmental Disorders, 23(2), 217–227.
- Meessen, J., Mainz, V., Gauggel, S., Volz-Sidiropoulou, E., Sütterlin, S., & Forkmann, T. (2016). The relationship between interoception and metacognition: A pilot study. *Journal of Psychophysiology*, 30(2), 76.
- Mehling, W. E., Price, C., Daubenmier, J. J., Acree, M., Bartmess, E., & Stewart, A. (2012). The multidimensional assessment of interoceptive awareness (MAIA). *PloS One*, 7(11), e48230.
- Mottron, L., Dawson, M., Soulieres, I., Hubert, B., & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders*, 36(1), 27–43.
- Mul, C.-l., Stagg, S. D., Herbelin, B., & Aspell, J. E. (2018). The feeling of me feeling for you: Interoception, Alexithymia and empathy in autism. *Journal of Autism and Developmental Disorders*. 1–15.
- Murphy, J., Millgate, E., Geary, H., Ichijo, E., Coll, M.-P., Brewer, R., ... Bird, G. (2018). Knowledge of resting heart rate mediates the relationship between intelligence and the heartbeat counting task. *Biological Psychology*, 133, 1–3.
- Nicholson, T., Williams, D., Grainger, C., Christensen, J., Calvo-Merino, B., & Gaigg, S. (2018). Interoceptive impairments do not lie at the heart of Autism or Alexithymia. *Journal of Abnormal Psychology*.
- Noel, J. P., Lytle, M., Cascio, C., & Wallace, M. T. (2018). Disrupted integration of exteroceptive and interoceptive signaling in autism spectrum disorder. *Autism Research*, 11(1), 194–205.
- O'Reilly, H., Lundqvist, D., Pigat, D., Baron, K., Fridenson, S., Tal, S., ... Baron-Cohen, S. (2012). *The EU-emotion stimulus set*. Cambridge, UK: Autism Research Centre, University of Cambridge.
- O'Reilly, H., Pigat, D., Fridenson, S., Berggren, S., Tal, S., Golan, O., ... Lundqvist, D. (2016). The EU-emotion stimulus set: A validation study. *Behavior Research Methods*, 48(2), 567–576.
- Palser, E. R., Fotopoulou, A., Pellicano, E., & Kilner, J. M. (2018). The link between interoceptive processing and anxiety in children diagnosed with autism spectrum disorder: Extending adult findings into a developmental sample. *Biological Psychology*, 136, 13–21. https://doi.org/10.1016/j.biopsycho.2018.05.003.
- Parker, J. D., Taylor, G. J., & Bagby, M. (1993). Alexithymia and the recognition of facial expressions of emotion. *Psychotherapy and Psychosomatics*, 59(3–4), 197–202.
- Peppé, S., Cleland, J., Gibbon, F., O'Hare, A., & Castilla, P. M. (2011). Expressive prosody in children with autism spectrum conditions. *Journal of Neurolinguistics*, 24(1), 41–53.
- Peppé, S., McCann, J., Gibbon, F., O'Hare, A., & Rutherford, M. (2007). Receptive and expressive prosodic ability in children with high-functioning autism. *Journal of Speech Language and Hearing Research*, 50(4), 1015–1028.
- Pollatos, O., Kirsch, W., & Schandry, R. (2005). Brain structures involved in interoceptive awareness and cardioafferent signal processing: A dipole source localization study. *Human Brain Mapping*, 26(1), 54–64.
- Pollatos, O., Traut-Mattausch, E., Schroeder, H., & Schandry, R. (2007). Interoceptive awareness mediates the relationship between anxiety and the intensity of unpleasant feelings. *Journal of Anxiety Disorders*, 21(7), 931–943.
- Porges, S. (1993). Body perception questionnaire: Laboratory of developmental assessment university of Maryland. *Pridobljeno*, 15(12), 2009.
- Prkachin, G. C., Casey, C., & Prkachin, K. M. (2009). Alexithymia and perception of facial expressions of emotion. *Personality and Individual Differences*, 46(4), 412–417.
- Rigby, S. N., Stoesz, B. M., & Jakobson, L. S. (2018). Empathy and face processing in adults with and without autism spectrum disorder. *Autism Research*.

Ring, C., & Brener, J. (2018). Heartbeat counting is unrelated to heartbeat detection: A comparison of methods to quantify interoception. *Psychophysiology*e13084.

- Ring, C., Brener, J., Knapp, K., & Mailloux, J. (2015). Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: A cautionary tale about interoceptive awareness. *Biological Psychology*, 104, 193–198.
- Rivet, T. T., & Matson, J. L. (2011). Review of gender differences in core symptomatology in autism spectrum disorders. *Research in Autism Spectrum Disorders*, 5(3), 957–976.
- Rosenblau, G., Kliemann, D., Dziobek, I., & Heekeren, H. R. (2017). Emotional prosody processing in autism spectrum disorder. *Social Cognitive and Affective Neuroscience*, 12(2), 224–239.
- Schandry, R. (1981). Heart beat perception and emotional experience. Psychophysiology, 18(4), 483–488.
- Schauder, K. B., Mash, L. E., Bryant, L. K., & Cascio, C. J. (2015). Interoceptive ability and body awareness in autism spectrum disorder. *Journal of Experimental Child Psychology*, 131, 193–200. https://doi.org/10.1016/j.jecp.2014.11.002.
- Schneider, K., Regenbogen, C., Pauly, K. D., Gossen, A., Schneider, D. A., Mevissen, L., ... Schneider, F. (2013). Evidence for gender-specific endophenotypes in high-functioning autism spectrum disorder during empathy. *Autism Research*, 6(6), 506–521.
- Schooler, J. W., Smallwood, J., Christoff, K., Handy, T. C., Reichle, E. D., & Sayette, M. A. (2011). Meta-awareness, perceptual decoupling and the wandering mind. *Trends in Cognitive Sciences*, 15(7), 319–326. https://doi.org/10.1016/j.tics.2011.05.006.
- Schulte-Rüther, M., Markowitsch, H. J., Shah, N. J., Fink, G. R., & Piefke, M. (2008). Gender differences in brain networks supporting empathy. *Neuroimage*, 42(1), 393–403.
- Schulz, S. M. (2016). Neural correlates of heart-focused interoception: A functional magnetic resonance imaging meta-analysis. *Philosophical Transactions Biological Sciences*, 371(1708), 20160018.
- Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. Trends in Cognitive Sciences, 17(11), 565–573.
- Seth, A. K., Suzuki, K., & Critchley, H. D. (2011). An interoceptive predictive coding model of conscious presence. *Frontiers in Psychology*, 2, 395. https://doi.org/10. 3389/fpsyg.2011.00395.
- Shah, P., Hall, R., Catmur, C., & Bird, G. (2016). Alexithymia, not autism, is associated with impaired interoception. *Cortex*, 81, 215–220.
- Shriberg, L. D., Paul, R., McSweeny, J. L., Klin, A., Cohen, D. J., & Volkmar, F. R. (2001). Speech and prosody characteristics of adolescents and adults with high-functioning autism and Asperger syndrome. *Journal of Speech Language and Hearing Research*,

44(5), 1097–1115.

- Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, 13(8), 334–340.
- Smith, M. J. L., Montagne, B., Perrett, D. L., Gill, M., & Gallagher, L. (2010). Detecting subtle facial emotion recognition deficits in high-functioning autism using dynamic stimuli of varying intensities. *Neuropsychologia*, 48(9), 2777–2781.
- Spielberger, C. D., Gorsuch, R. L., & Lushene, R. E. (1970). Manual for the state-trait anxiety inventory.
- Terasawa, Y., Shibata, M., Moriguchi, Y., & Umeda, S. (2012). Anterior insular cortex mediates bodily sensibility and social anxiety. *Social Cognitive and Affective Neuroscience*, 8(3), 259–266.
- Tracy, J. L., & Randles, D. (2011). Four models of basic emotions: A review of Ekman and Cordaro, Izard, Levenson, and Panksepp and Watt. *Emotion Review*, 3(4), 397–405.
- Uddin, L. Q. (2015). Salience processing and insular cortical function and dysfunction. Nature Reviews Neuroscience, 16(1), 55–61.
- Wang, J.-E., & Tsao, F.-M. (2015). Emotional prosody perception and its association with pragmatic language in school-aged children with high-function autism. *Research in Developmental Disabilities*, 37, 162–170.
- Watanabe, T., Yahata, N., Abe, O., Kuwabara, H., Inoue, H., Takano, Y., ... Takao, H. (2012). Diminished medial prefrontal activity behind autistic social judgments of incongruent information. *PloS One*, 7(6), e39561.
- Whitehead, W. E., Drescher, V. M., Heiman, P., & Blackwell, B. (1977). Relation of heart rate control to heartbeat perception. *Biofeedback and Self-Regulation*, 2(4), 371–392.
- 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.
- Wiens, S., Mezzacappa, E. S., & Katkin, E. S. (2000). Heartbeat detection and the experience of emotions. Cognition & Emotion, 14(3), 417–427. https://doi.org/10.1080/ 026999300378905.
- Williams, D. L., Goldstein, G., & Minshew, N. J. (2006). Neuropsychologic functioning in children with autism: Further evidence for disordered complex information-processing. *Child Neuropsychology*, 12(4–5), 279–298.
- Xu, J., Wang, H., Zhang, L., Xu, Z., Li, T., Zhou, Z., ... Hu, Q. (2018). Both hypo-connectivity and hyper-connectivity of the insular subregions associated with severity in children with autism Spectrum disorders. *Frontiers in Neuroscience*, 12, 234.
- Yoris, A., Esteves, S., Couto, B., Melloni, M., Kichic, R., Cetkovich, M., ... Ibanez, A. (2015). The roles of interoceptive sensitivity and metacognitive interoception in panic. *Behavioral and Brain Functions*, 11(1), 14.