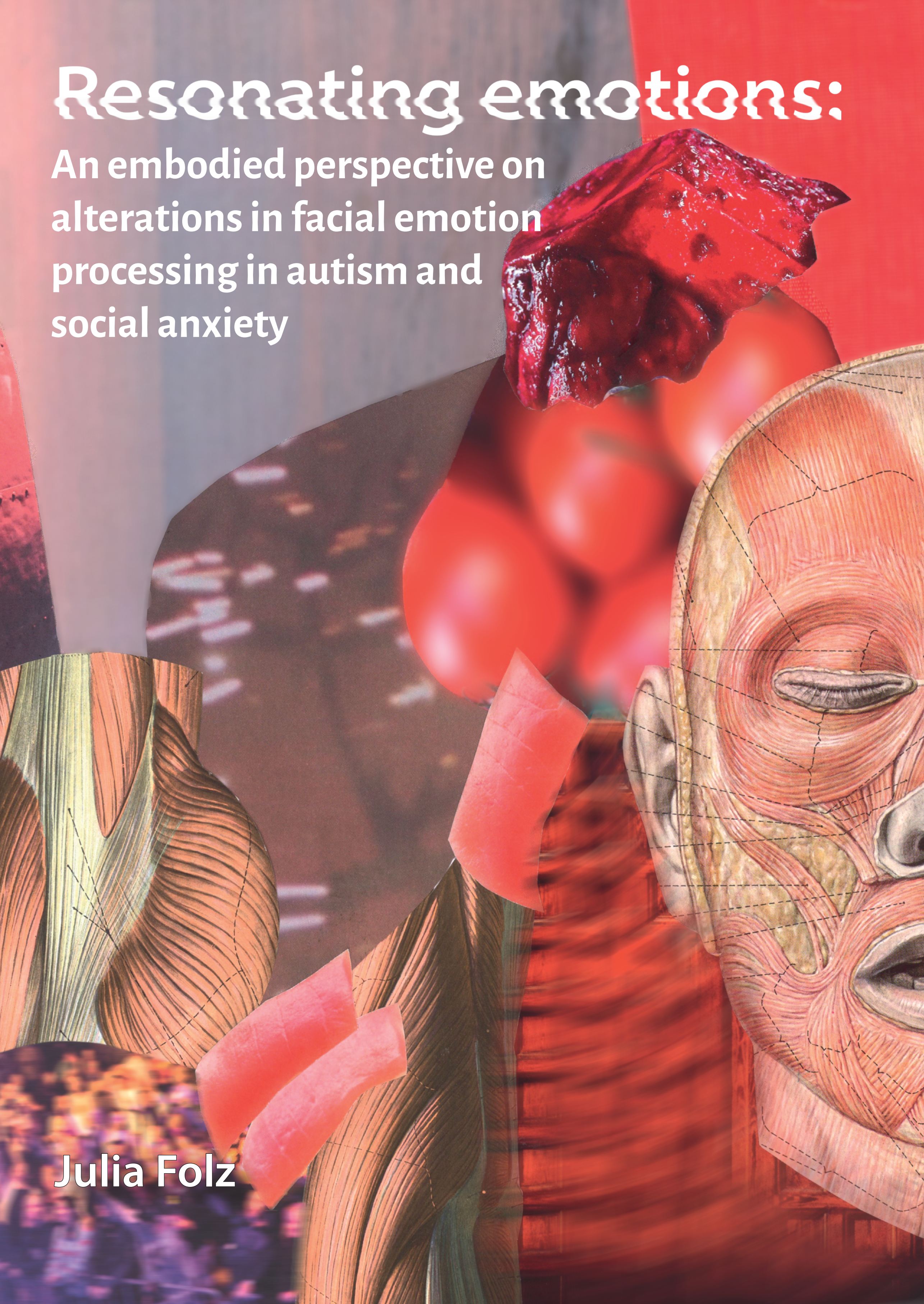
Resonating emotions:

An embodied perspective on alterations in facial emotion processing in autism and social anxiety



Julia Folz

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Colofon

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Julia Folz

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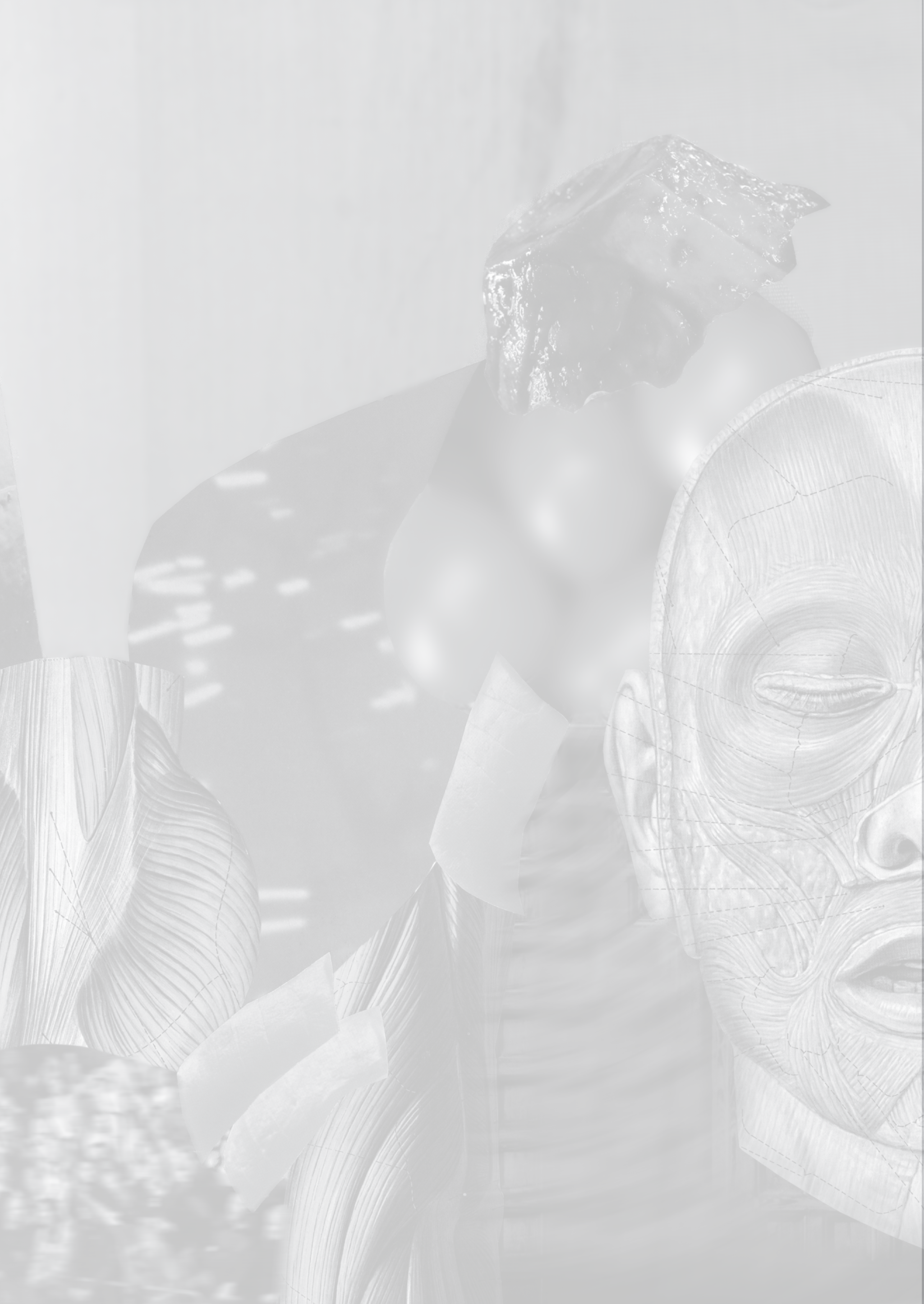
Preface

In 2018, Mariska Kret received a VIDI grant (number 016.VIDI.185.036) by the Dutch research Council (Nederlandse Organisatie voor Wetenschappelijk Onderzoek) to investigate "Emotional contagion in autism and social anxiety". For the practical implementation of the research, she advertised a PhD position, zooming in on the bodily signature of emotional social exchanges. Especially one part of the project, which involved real interactions with simultaneous physiological recordings of both interactants, caught my interest. Following my successful application, we decided that it should become the focus of my dissertation.

Starting as first PhD student on a new, highly complex project typically comes with various challenges. Some of them were expected, like setting up and piloting all tasks in a student population, learning diagnostic procedures, or applying for ethical approval with the Medical Ethics Committee. Some other challenges could not be easily predicted, such as long delays in the application process for ethical approval or changes in supervisors. Yet, the biggest challenge that I, and every other individual at that time, had to face was the Covid-19 pandemic. There is probably no need to go into the details of the detrimental effects that the pandemic had on daily life and well-being. It had, however, also a strong impact on the course of my PhD project. For long time periods, conducting research, particularly real interaction studies and with vulnerable populations, seemed impossible.

Fortunately, I had already collected data for the non-interactive parts of the project with student samples, which I could analyze. In addition, I was very lucky to be surrounded by great collaborators and support staff. Together with my fellow PhD student Fabiola Diana and the technical support of Leiden University, we developed procedures to continue data collection and even prepare interactive studies in Leiden when the pandemic was slowly waning. Moreover, in sporadic visits (when possible) and continuous video calls, my fellow PhD student Kristina Nikic and I managed to prepare the data collection at our collaborators' testing site, at the LVR hospital in Essen (Germany). The great efforts of our German collaborators, under the supervision of Katja Koelkebeck, rendered the inclusion of a dissertation chapter with a clinical sample possible. Although I had to let go of my initial goal to focus on the part of the project including real social interactions, I could still realize my interests within the project. Carried by the flexibility and trust of my promotor Mariska Kret, I zoomed in on the role of the ability and inclination to sense and interpret internal signals (i.e., interoception) in emotion perception. This addition seemed not only the logical consequence of my embodied perspective on facial emotion processing but also provided novel insights to the existing literature. Looking back on the journey, besides experiences of frustration, the challenges pushed me to growth in directions that I would not have imagined. The results are reflected in the current dissertation, and this preface could hopefully offer the reader useful contextual information.



Chapter 1

General Introduction

The need to form meaningful relationships with others is an integral part of human nature (Baumeister & Leary, 1995). Social interactions - everyday instances reflecting this need – are known to play an important role in determining an individual's well-being and their life satisfaction (Diener et al., 2018; Sun et al., 2020). In interactions, people share their emotional and mental states, both verbally and non-verbally, with others. An alignment to each other facilitates mutual understanding, and allows for supporting each other in regulating imbalanced emotional states or in updating inaccurate beliefs. The ability to "tune in" to another person is an important resource in daily social functioning, which is described to be "impaired"[1] in the DSM-V diagnostic criteria of both Social Anxiety Disorder and Autism Spectrum Disorder (American Psychiatric Association, 2013). Alterations in experiences and behaviour, similar to those described in individuals with a diagnosis of autism or social anxiety, can also be observed in individuals without a diagnosis (see Box 1 for a description of the two conditions and the association with trait levels). The present dissertation therefore includes research in both non-diagnosed individuals with varying autistic trait levels and social anxiety trait levels, and individuals with a diagnosis of either Social Anxiety Disorder (referred to as "individuals with social anxiety") or Autism Spectrum Disorder (referred to as "individuals on the autism spectrum") to approach a better understanding of potential alterations in processes which may contribute to social interaction difficulties in the two conditions.

Difficulties in Social Interactions in Autism and Social Anxiety

Research on social functioning in social anxiety and autism highlights alterations in social cognition and behaviour, which are linked to a lower quality of life in the two conditions (S. Y. Kim & Bottema-Beutel, 2019; Oakley et al., 2020; Olatunji et al., 2007). For example, altered trust in social interactions has been described in both autism and social anxiety. While individuals on the autism spectrum are less influenced by another persons' looks or their prosocial behaviour in trust decisions

1 Deficit-oriented language (e.g., "impairments", "Disorder") is used here in order to adhere to the clinical diagnostic criteria. Yet, I would like to highlight that I do not believe social interaction difficulties to be necessarily the result of one individual's "impairment". Following a neurodiversity perspective, individuals differ in their cognitive styles, which also reflects in interpersonal communication. This idea will be elaborated on in more detail in the discussion.

(Ewing et al., 2015; Hooper et al., 2019; Maurer et al., 2018), individuals with social anxiety are less inclined to trust in general (Rodebaugh et al., 2016, 2017) compared to controls. Moreover, both individuals on the autism spectrum and individuals with social anxiety perceive themselves as less socially competent and liked (Voncken et al., 2020; Williamson et al., 2008). There is some evidence that this self-perception matches others' impressions: they actually make less positive impressions in interactions compared to controls, which is also reflected in others' relatively lower wish for future interactions (Morrison et al., 2020; Voncken & Bögels, 2008). Yet, specifically in the case of social anxiety, negative self-perceptions are highly exaggerated compared to negative perceptions by others (Christensen et al., 2003). Generalizing negative beliefs about one's abilities, which are formed in interactions with others, might tremendously contribute to a reduced confidence in social skills and affect social functioning in social anxiety (Müller-Pinzler et al., 2019).

Some theoretical perspectives suggest that impairments in social functioning would arise from a decreased social motivation. In the case of autism, the social motivation theory suggests that, overall, less attention would be employed to social information, which has a lower reward value (Chevallier et al., 2012; however see Bottini, 2018). In the case of social anxiety, theoretical accounts propose that reduced social motivation would be rooted in behavioural inhibition, that is, the temperamental trait to avoid unknown people and novel situations which elicit distress (Fox et al., 2021; Kimbrel et al., 2012), or in overvaluing social rank over affiliation in social situations, hindering the approach of others (Gilboa-Schechtman, 2020). Importantly, both individuals with social anxiety and a substantial share of individuals on the autism spectrum do not report a reduced need to interact and build relations with others, and they also participate in social life (L. H. Brown et al., 2007; Chan et al., 2023). The quality of social interactions is, however, perceived to be lower by individuals with social anxiety compared to controls (Villanueva et al., 2021), and they report to prefer to be alone in the context of unfamiliar others (L. H. Brown et al., 2007). Social interaction difficulties in autism have been reflected in less involvement in peer relationships as well as in social and recreational activities (Orsmond et al., 2004). Hence, alterations in social functioning occur in both conditions and seem to hamper forming new, meaningful relationships with others. While the general profiles as well as theoretical perspectives on the aetiology of social anxiety and autism

BOX 1 | Description of Autism Spectrum Disorder, Social Anxiety Disorder, and Associated Trait Levels

According to the DSM-V (American Psychiatric Association, 2013), Social Anxiety Disorder (SAD; or social phobia) belongs to the cluster of Anxiety Disorders, which are mental health conditions characterized by excessive and uncontrollable fear and anxiety in everyday life situations. Within this cluster, SAD manifests specifically in a disproportionate fear and avoidance of social situations, which is based on fears of evaluation by others, and causes substantial distress to the individual. Autism Spectrum Disorder (ASD) is a neurodevelopmental condition characterized by "impairments" in social communication, such as eye contact or social reciprocity, and restricted, repetitive behaviours, such as stereotypic movements or sensory interests, which already manifest in early development. As reduced intellectual development (e.g., being less verbal) complicates the study of social functioning in autism, most research (including this thesis) includes individuals on the autism spectrum with intellectual ability that is comparable to control participants to target alterations specifically linked to social cognition and behaviour.

Alterations in experiences and behaviour that show similarities to those described in individuals with a diagnosis of autism or social anxiety present themselves to varying degrees in the general population. These characteristics are commonly referred to as autistic traits or social anxiety traits (Rapee & Spence, 2004; E. B. Robinson et al., 2011). To give an example, people with high autistic trait levels can find it difficult to infer others' intentions or have a hard time deviating from established routines. In the case of social anxiety, people with high trait levels can, for example, experience anxiety when meeting strangers or avoid giving a speech in front of others. Individuals with high social anxiety trait levels but no diagnosis mainly differ from individuals with social anxiety in the degree to which symptoms impact their daily life (American Psychiatric Association, 2013). Experiences of individuals on the autism spectrum, in contrast, can be qualitatively different compared to experiences of neurotypical individuals with high autistic trait levels (Sasson & Bottema-Beutel, 2022). Yet, assessing trait levels in individuals without the respective condition can allow researchers to approach phenomena related to autism and social anxiety, and can inform studies in the two conditions, without immediately involving individuals with a diagnosis.

co-occurs in autism, with comorbidity rates ranging between 16.6% - 50% (Bejerot et al., 2014; Maddox & White, 2015; van Steensel et al., 2011). In order to get a better idea of potential shared and distinct mechanisms underlying alterations in social functioning in autism and social anxiety, a fine-grained investigation of alterations in processing social information is required. The present dissertation therefore zooms in on the perception and the resonance of others' nonverbal emotional expressions in both varying trait levels associated with autism and social anxiety in non-diagnosed individuals as well as in the two conditions.

Perception of Nonverbal Signals of Emotions in Autism and Social Anxiety

Non-verbal expressions of emotions, such as facial displays, body postures, movements, vocalizations, or gestures (A. Cowen et al., 2019; Dael et al., 2013; de Gelder, 2006; Ekman, 1993; Sauter et al., 2010; Witkower & Tracy, 2019), are relevant signals in guiding social interactions, by providing information about the expressor's emotional state. This social-communicative function is, however, not considered the original function of emotional expressions. It is proposed to have emerged in socially complex animals to transfer information, going beyond a pure physiological function (Shariff & Tracy, 2011; Tracy et al., 2015). Namely, from an evolutionary perspective, emotions primarily served to promote survival, as specialized modes that allow the organism to adaptively respond to the environment (Nesse, 1990; Tooby & Cosmides, 1990). Here, basic emotion theory highlights a set of fundamental, evolutionary-adaptive emotions (commonly: anger, fear, happiness, surprise, sadness and disgust), which are distinct to each other and share differences to related phenomena, such as moods (Ekman, 1992). One of the shared characteristics of these emotions is their emotion-specific expression, which has primarily been described in the face in humans, including the definition of specific muscle activation patterns (Friesen & Ekman, 1983). Opposing the idea of emotions as universal, hardwired modes, constructionist perspectives point out the uniqueness of each emotional experience. They propose that emotions are constructed based on an individuals' past experiences, their current states and the environment that they are in, thus never resulting in the exactly same experience (see Barrett, 2006; Russell, 2003). While the debate on the nature of emotions is ever ongoing between proponents of the two different perspectives, many scholars acknowledge a functional basis, which allows for a categorization of emotional states, without neglecting the uniqueness of experiences, based on individual characteristics or contextual factors (see also Scarantino & Griffiths, 2011; van Heijst et al., 2023). In the current dissertation, I examine emotional expressions in their social-communicative function more closely, zooming in on individual differences in their perception and interpretation that are associated with autism and social anxiety. In line with most research in this field, my main focus is on the processing of distinct facial displays of emotions, following basic emotion categories. For these "prototypical" expressions, alterations associated with autism and social anxiety have been described at various processing stages and various levels of description.

While emotional expressions are known to automatically capture and hold attention in general (Carretié, 2014), both individuals on the autism spectrum and individuals with social anxiety show altered patterns of attentional deployment. Following predictions of theoretical models, such as the Relevance Detection theory (Zalla & Sperduti, 2013) or the two-pathway model (Cuve et al., 2018), individuals on the autism spectrum tend to avoid faces, and specifically the eye region, to regulate arousal. According to the Relevance Detection theory, this avoidance stems from a hyper-activation of the amygdala in response to salient stimuli, such as others' eyes, which results in unpleasantly high arousal levels. Next to this explanation, the two-pathway model (Cuve et al., 2018) proposes a lower automatic engagement with the eye region in some individuals on the autism spectrum, accompanied by lower arousal levels and less attention to the eyes, as second path. Importantly, avoiding another individual's eyes seems to negatively impact the processing of their facially displayed emotions, as alterations in gaze, including an avoidance of the eye region, have been linked to a lower emotion recognition performance in individuals on the autism spectrum compared to control participants (Kliemann et al., 2010). In contrast, angry facial expressions have repeatedly been shown to affect both initial and sustained attention more strongly in individuals with social anxiety compared to controls (Clauss et al., 2022; Lazarov et al., 2021; Mogg, Bradley, et al., 2004). The proposed explanation for this phenomenon is that they represent social threat (i.e., negative evaluations), as described in the cognitive behavioral model of social anxiety by Rapee & Heimberg (most recent update: Heimberg et al., 2010), which highlights an increased vigilance to external social cues.

In addition to attentional alterations, individuals on the autism spectrum and individuals with social anxiety tend to interpret observed facial emotional expressions differently than controls. Namely, individuals on the autism spectrum may perceive emotional expressions as less intense (Tseng et al., 2014), have more difficulties in recognizing emotions (Yeung, 2022), and struggle in inferring mental states of others (Quinde-Zlibut et al., 2022) when compared to controls. These findings have been conceptualized as "impairments" in traditional models such as the Theory of Mind model (ToM model; Baron-Cohen et al., 1985) and the broken mirror hypothesis (Ramachandran & Oberman, 2006; Southgate & Hamilton, 2008; J. H. G. Williams et al., 2001): According to ToM model, children on the autism spectrum would be less able to represent others' mental states and predict their behaviour, as they show difficulties in inferring another individual's mental state about a third person (second-order ToM; however see Tager-Flusberg, 2007). In contrast to this rather conceptual model, the broken mirror hypothesis links alterations in behaviour to alterations in neural activity that have been observed in autism. Difficulties in imitation, and other processes requiring attunement to other individuals, are proposed to stem from a dysfunction of a brain system, the mirror neuron system, whose activity reflects simulations of observed actions. Novel perspectives, in contrast, focus on identifying different strategies that individuals on the autism spectrum employ in processing others' emotions (Arnaud, 2020; Keating et al., 2023; Rutherford & McIntosh, 2007). In individuals with social anxiety, negatively-biased processing of facial information(Machado-de-Sousa et al., 2010) is assumed to explain observations such as a higher sensitivity towards negative expressions (Gutiérrez-García & Calvo, 2017a; Joormann & Gotlib, 2006) and a higher misattribution of negative affect to neutral faces (Peschard & Philippot, 2017). Although individuals with social anxiety do not necessarily recognize expressions of others worse than controls, they have difficulties interpreting them (Buhlmann et al., 2015). In those lines, individuals with social anxiety are less accurate in inferring complex mental states of others (i.e., cognitive empathy) compared to controls, whereas the sharing of other's emotions (i.e., affective empathy) is comparable or under specific circumstances even enhanced (Alvi et al., 2020; Pittelkow et al., 2021). Taken together, individuals with social anxiety specifically seem to be receptive to negative facial expressions and biased in the interpretation of others' emotional displays. Individuals on the autism spectrum, in contrast, seem to attend to (emotional) facial displays less and process them differently, which can result in a misunderstanding of others' emotional states. Relevant alterations in processing facial information, thus, likely occur at various processing stages in autism and social anxiety (e.g., attention, interpretation), affecting different levels of description (e.g., experience, physiology). Importantly, the covered processing stages and levels in this dissertation are neither conclusive nor do they occur in a consecutive or hierarchical order, as one might infer. Understanding others' emotions is a highly complex, dynamic and versatile phenomenon, in which various individual and environmental factors can play a role.

Resonance of Observed Emotional Expressions in Autism and Social Anxiety

Humans "feel" emotions in their bodies: they consistently link distinct bodily states to specific emotional states (Nummenmaa et al., 2014). In those lines, various seminal emotion theories, such as the James-Lange-Theory (James, 1884; Lange & Kurella, 1887) or the Somatic Marker Hypothesis (Damasio, 1996) among others (e.g., Levenson, 2003), highlight the role of physiological feedback in the experience of emotions. Here, automatically evoked activity changes in targets of both the somatic nervous system (e.g., facial muscles) and the autonomic nervous system (e.g., the heart) can inform consciously experienced emotional states (Buck, 1980; Critchley, 2009). Next to emotion-specific facial muscle configurations (Friesen & Ekman, 1983), distinct emotional states also show consistent (de-)activations in different measures of autonomic nervous system activity (Friedman, 2010; Kreibig, 2010; Levenson, 2014), yet no clearly distinguishable patterns (Kragel & LaBar, 2013; McGinley & Friedman, 2017; Siegel et al., 2018). Crucially, physiological response patterns in observers of emotional expressions are, specifically when it comes to facial expressions (Wingenbach et al., 2020), highly similar to the direct experience of the observed emotional state. They "resonate" in the observer (Lomas et al., 2022). This correspondence is integral to the broader idea of emotional contagion, that is an automatic alignment to another person's emotional state in physiology, behaviour and experience (E. Hatfield et al., 1993; Prochazkova & Kret, 2017). From the functional perspective, the internal simulation of an observed state leads to a better understanding of the other, makes them more predictable and likely results in smoother interactions (Arnold & Winkielman, 2020; Niedenthal, 2007; Preston & de Waal, 2002; Wood et al., 2016). In turn, a reduced simulation of others' emotions or altered physiological feedback interferes with this function, and might contribute to difficulties in social interactions, and social functioning more broadly, in autism and social anxiety (Alkire et al., 2021).

Research on spontaneous facial mimicry, that is the mirroring of observed facial expressions, has indeed shown that individuals on the autism spectrum mimic expressions of others less (Davies et al., 2016), or differently (Oberman et al., 2009; Weiss et al., 2019), than controls. Some studies also report reduced physiological arousal in response to others' emotions (Hubert et al., 2009; Keil et al., 2018; however see Dijkhuis et al., 2019; Mathersul et al., 2013). For individuals with social anxiety, results regarding spontaneous alterations in facial mimicry (e.g., Dijk et al., 2018; Vrana & Gross, 2004) as well as physiological arousal responses to emotional expressions (e.g., Dimberg & Thunberg, 2007; Tsunoda et al., 2008) are less conclusive. Here, the presence of a social context and its effects on information processing and behaviour might play a crucial role (Rapee & Heimberg, 1997). Namely, individuals with social anxiety care more about behaving socially desirable and overestimate the visibility of their actual physiological arousal in a social context (Edelmann & Baker, 2002; Nikolić et al., 2015), which may lead them to control their expressions more strongly than control participants (Dijk, Fischer, et al., 2018) and act rigidly, thereby limiting the resonance of others' expressions in their own body. In those lines, even if others emotions' would resonate similarly in the two conditions compared to controls, this "feedback", may not necessarily be integrated to a similar degree or in a similar way.

Sensation of Embodied Emotions in Autism and Social Anxiety

Individuals indeed vary widely in how strongly signals from their bodies link to the perception of their own as well as observed emotional states (Coles et al., 2019; Holland et al., 2020). Recent approaches that aim for a mechanistic understanding of individual differences in emotion processing, therefore, investigate the role of interoception (Critchley & Garfinkel, 2017), that is the sensation, integration, interpretation and regulation of internal signals (W. G. Chen et al., 2021). Corresponding to this definition, interoceptive processes can be described at different levels of processing ("dimensions"), such as the strength of the afferent signal, as well as for different bodily systems ("axis"), such as the cardiovascular system (Suksasilp & Garfinkel, 2022). Existing theoretical frameworks focus on different aspects to describe individual differences in interoceptive processing. In the dimensional approach by Garfinkel and colleagues (2016), three dissociable measures of interoception are distinguished (see also Forkmann et al., 2016), namely interoceptive accuracy (i.e., the objective accuracy in the detection of interoceptive signals), interoceptive sensibility (i.e., the self-reported, subjective tendency to focus and be aware of interoceptive signals) and interoceptive awareness (i.e., the ability to assess one's interoceptive accuracy correctly).

Importantly, the self-reported tendency to attend to bodily signals in daily life does not necessarily translate to a more accurate detection, as the above-mentioned overestimation of bodily responses in social anxiety illustrates. To capture this dissociation, Murphy and colleagues (2019) developed a 2x2 factor model of interoceptive ability, with the first factor ('What is measured?') distinguishing between accuracy and attention. The second factor ('How is it measured?') contrasts beliefs regarding one's performance (i.e., self-reports) with one's actual performance (i.e., objective measures). Although individuals with Anxiety Disorders overall (Domschke et al., 2010) or non-diagnosed individuals with high social anxiety trait levels (Stevens et al., 2011) tend to be more accurate in sensing their heartbeats in experimental tasks than control participants, individuals with social anxiety specifically seem to perform as well (Antony et al., 1995) or even worse (Gaebler et al., 2013) than control participants. Similarly, individuals on the autism spectrum perform worse in interoception tasks compared to controls (Failla et al., 2020; Garfinkel et al., 2016). At the same time, some individuals on the autism spectrum report to overperceive specific body signals (Garfinkel et al., 2016), while having difficulties in their integration to a coherent percept and in their interpretation (e.g., Fiene et al., 2018). This observation has been delineated in the framework of the weak (central) coherence account of autism (Happé & Frith, 2006), which describes a bias to processing local features (here: distinct body signals) and difficulties to integrating those to a global form (here: physiological state; see T. R. Hatfield et al., 2019). The overrepresentation of distinct body signals is also central to a predictive coding perspective on altered interoceptive processing in autism, namely the idea of highly inflexible precise prediction errors (Van de Cruys et al., 2017). Simplified, by constantly reinforcing irrelevant body signals (via high precision), body signals of actual interest do not "stand out". In contrast to this altered integration of low-level information (bottom-up), top-down processing rather seems to be affected in anxiety, operationalizing it as "altered interoceptive state[s] as a consequence of noisily amplified self-referential interoceptive predictive belief states" (Paulus & Stein, 2010, p. 451). The idea that self biases in social anxiety would result from discrepancies in expected and actual physiological states was recently elaborated in detail in a predictive coding framework (Gerrans & Murray, 2020), and currently seems the most agreed-upon explanation of biased perception of physiological responses in social anxiety. Although alterations in sensing bodily signals, including their potential underlying mechanism(s), have been described in the literature on autism and social anxiety, studies investigating the role of these alterations in processing others' emotions are scarce. There is only some evidence that (changes in) arousal levels in individuals on the autism spectrum would indeed be less strongly linked to sharing other emotions compared to controls (Dijkhuis et al., 2019; Mathersul et al., 2013). Reduced empathy in autism has further been associated with lower objectively-measured interoceptive accuracy (Mul et al., 2018), yet not consistently (Butera et al., 2023).

Employment of More Naturalistic Stimuli in Facial Emotion Perception Research

Even though humans are confronted with a broad variety of rich emotional facial expressions in daily life, research on facial emotion perception has mostly employed static images of exaggerated and posed stimuli (Kret, 2015). In order to gain more valid insights into processing others' emotions in a laboratory setting, novel stimulus sets with more naturalistic emotional expressions have recently become more popular (Dobs et al., 2018; Krumhuber et al., 2017). The advantage of their usage has already been demonstrated in several studies in the general population. For example, dynamic (versus static) facial displays emotion elicit stronger responses on multiple levels, including subjective reports (Krumhuber et al., 2013), physiological resonance (Rymarczyk et al., 2011), as well as neuronal responses (Schultz & Pilz, 2009). Dynamic information in facial emotion recognition seems to become particularly relevant when individuals are exposed to subtle and ambiguous displays (Ambadar et al., 2005; Krumhuber et al., 2013), whereas evidence for a potential advantage when exposed to prototypical facial expressions is inconsistent (see Sauter & Fischer, 2018).

Dynamic information might, however, not facilitate processing for all observers of emotional facial expressions. Individuals on the autism spectrum do not seem to benefit from the addition of dynamic information in recognizing emotions, but have rather been found to recognize dynamic sad facial expressions less accurately than static ones (Enticott et al., 2014). This could be due to differences in internal representations of facial motion associated with specific emotional expressions in individuals on the autism spectrum compared to controls (e.g., for anger expression, see Keating et al., 2021). Furthermore, while individuals with high social anxiety trait levels within the general population showed an advantage in recognizing static facial expressions of anger, this was not the case for dynamic expressions of anger (Torro-Alves et al., 2016). Thus, using richer facial emotional expressions as stimuli in laboratory settings might allow to tap into more diverse and relevant alterations in facial emotion perception associated with autism and social anxiety. An additional path for facial emotion perception research to obtain higher ecological validity is to study the role of more subtle indicators of emotional experiences. Cues of emotional arousal, such as a blush, tears or the dilation of pupils, are less easily controlled than facial muscle (de-)activations, and can hence be seen as an even more pure visible sign of emotions in others (Kret, 2015). Studying changes in indicators of autonomic nervous system activity associated with the expressions of these visible cues (e.g., pupil size, facial reddening) can provide promising insights in the alignment in (emotional) arousal.

Outline of the Dissertation

Understanding others' emotions in interactions is crucial in forming social bonds which eventually contribute to an individual's well-being. Both individuals on the autism spectrum and individuals with social anxiety have difficulties in interactions with others, and past research suggests that they also differ in how they perceive and respond to others' emotions. So far, however, most studies have examined alterations associated with either autism or social anxiety (trait levels), complicating to unveil shared and distinct alterations. Often, they have focussed on alterations on one level of description (e.g., physiological resonance versus subjective interpretation), without considering potential links between levels. Addressing these limitations, the present dissertation aims to provide a more integrative understanding of alterations in the perception, resonance and interpretation of other individual's (facial) emotional expressions in autism and social anxiety (trait levels). As this is a complex process, the different chapters of the dissertation focus on relevant factors in different processing stages and at different levels of description, as well as the links between them.

Chapter 2 explores differences in attentional tendencies towards facial emotional expression that are associated with higher autism and social anxiety trait levels in a large, heterogenous sample, using a so-called dot-probe paradigm. By tracing systematic differences in responding to briefly presented facial emotional expressions, the goal of this chapter is to capture automatic and fast alterations in reactions to others' emotions, that are not heavily influenced by elaborate processing. Furthermore, going beyond previous research, I include a variety of distinct facial emotional expressions, which allows to differentiate between emotion-general and emotion-specific attentional tendencies.

In Chapter 3, I examine bodily responses to others' emotional expressions in observers as well as their interpretations, covering different levels of description in facial emotion perception. Since a comprehensive overview of the bodily resonance of diverse emotional expressions in non-clinical samples has been lacking in the literature, my aim was to gain a better understanding of this phenomenon, without considering the two conditions, as a first step. My examination includes (1) distinct facial emotional cues (tears, blushing and dilated pupils) and emotional expressions (anger, happiness, sadness, fear), the latter expressed via different modalities (face versus body), (2) different physiological measures (facial muscle activity, skin conductance and cheek temperature), as well as (3) different interpretation indices (emotion recognition, perceived intensity of others' emotions and confidence in own judgement).

In line with the broader literature, the resonance of facial emotional expressions shows to be most robust and distinguishable between different emotions in facial muscle (de-) activations in Chapter 3. It, therefore, seems most promising to focus on alterations in facial mimicry, as well as in its link to subjective facial emotion perception, in autism and social anxiety. In Chapter 4, I take a first step toward this goal by examining individual differences related to autistic and social anxiety trait levels in a student population, as indication of potential alterations in the two conditions. Processing of social information can be influenced by beliefs about one's abilities, as specifically highlighted in theories on social anxiety. This has, however, only rarely been examined in an emotion recognition context, and even less so in relation to the two conditions. Hence, I additionally investigate systematic variations related to autistic and social anxiety trait levels in how confidence in emotion recognition is linked to actual recognition performance. In contrast to the posed facial expressions used in most previous research, I use standardized videos of spontaneous facial emotional expressions as stimuli, increasing the ecological validity of computer-based facial emotion recognition paradigms.

Chapter 5 examines a potential mechanism in altered integration of physiological information in emotion processing, namely interoception. Difficulties in interoception are broadly described in the literature on autism, but their role in interpreting others' emotional expressions is not well understood yet. In this chapter, I aim to quantify the degree to which different measures of interoception can explain altered perception of specific facial emotional expressions with higher autistic trait levels in the general population. In order to increase the explanatory power of my results, I replicate the initial online study in the lab, using the same task, and I add objective measures of facial muscle responses to observed expressions (i.e., mimicry) and of interoceptive accuracy.

In the previous chapters of this dissertation (apart from Chapter 2), I thoroughly examine alterations in facial emotion processing at different processing stages and at different levels of description in relation to autistic and social anxiety trait levels in the general population. Chapter 6 allows to test the thereupon based predictions in a clinical sample, that is, in individuals with a diagnosis of either Autism Spectrum Disorder or Social Anxiety Disorder. I specifically focus on the link between the physiological resonance of facial expressions, indexed by facial muscle activations and skin conductance, and facial emotion perception (recognition, confidence in recognition and perceived intensity), as well as the role of interoception therewithin. In order to be able to infer both the presence as well as the absence of differences in the two groups compared to the control group, I conduct Bayesian analyses next to Frequentist analyses.

Together, the five chapters present novel insights in the putative relevance of the spontaneous embodiment of others' emotions, including the sensation and integration of this physiological resonance, in alterations in facial emotion processing in autism and social anxiety (trait levels).

Chapter 2:

Who Gets Caught by the Emotion? Attentional Biases toward Emotional Facial Expressions and Their Link to Social Anxiety and Autistic Traits

Abstract

The emotional facial expressions of other individuals are a valuable information source in adapting behaviour to situational demands, and have been found to receive prioritized attention. Yet, enhanced attentional biases, such as a bias to social threat in Social Anxiety Disorder (SAD), or blunted attention to emotional information, as assumed in Autism Spectrum Disorder (ASD), can easily become maladaptive in daily life. In order to investigate individual differences in attentional biases toward different emotional expressions (angry, happy, sad, and fearful versus neutral) and their links to social anxiety and autistic traits, we tested 104 healthy participants with an emotional dot-probe paradigm on a touch screen, and measured clinical trait levels associated with ASD and SAD. While confirming the presence of attentional biases toward all emotional expressions, we did not find robust evidence for systematic links between these biases and either clinical trait dimension. Only an exploratory Bayesian analysis pointed to a less pronounced bias towards happy facial expressions with higher autistic trait levels. Moreover, a closer examination of the attentional bias towards angry facial expressions suggested that alterations in this bias might depend on a complex interplay between both trait dimensions. Novel approaches in the assessment of attentional biases might yield the potential to describe disorder-specific biases in attention to emotions more validly.

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Data availability statement:
The datasets and materials generated and/or analysed during the current study are available on Dataverse NL: https://doi.org/10.34894/UVQHHD

Supplementary material:

Online Resource 1

Online Resource 2

Living in a world rich in (visual) stimulation, the human perceptual system requires guidance to filter the environment for crucial information. Emotional stimuli have been shown to strongly capture and hold attention in various modalities and impact subsequent behaviour (Carretié, 2014). Already in the first years of life, infants use their caregivers' emotional expressions to evaluate the current situation, which is commonly referred to as social referencing (e.g., Möller et al., 2014). Further, also in some non-human primates, emotional expressions of conspecifics have been found to receive prioritized attention, resulting in faster responding (e.g., Kret et al., 2016; van Berlo et al., 2020). Thus, the phenomenon of attention being automatically directed to emotional expressions of others seems to be a deeply-rooted, adaptive mechanism in social animals.

Experimental paradigms have confirmed attentional biases toward various emotional facial expressions and body postures in healthy individuals (Bradley et al., 1997; Carlson & Mujica-Parodi, 2015; Valk et al., 2015; Wirth & Wentura, 2020).In individuals with a diagnosis of Autism Spectrum Disorder (ASD) or Social Anxiety Disorder (SAD), alterations in attention to emotional information have been suggested as one potential mechanism underlying social interaction difficulties (Bantin et al., 2016a; Kliemann et al., 2010). However, research on altered attentional biases in these clinical conditions has mainly focused on social threat perception (i.e., displays of anger), whereas humans are exposed to a broad range of emotional displays in daily life. Moreover, different mechanisms have been proposed to underlie altered attention to emotion in the two clinical conditions. With the current study, we therefore aimed to take a step towards the identification of potential systematic alterations in the attention to emotional expressions in ASD and SAD by examining the link between variations in trait levels associated with the two conditions and attentional biases toward different emotional expressions.

Attention to Emotional Facial Expressions and the Dot-probe Paradigm

In the non-verbal communication of affect, facial expressions are particularly salient and have been shown to effectively capture attention. Most studies so far have focussed on biases to negative stimuli and have identified an "anger superiority effect" (Hansen & Hansen, 1988). This effect describes the rapid and preferential detection of angry faces among others, highlighting the importance of threatening information. Yet, recent studies have shown that also positive stimuli, including smiling faces, attract attention compared to neutral stimuli

(Pool et al., 2016). To systematically investigate biased attention to certain stimuli, namely biases to threat stimuli in individuals with a depression or anxiety disorder, the dot-probe task was developed (MacLeod et al., 1986). Since then, it has been used to investigate a variety of biases to a variety of stimuli in different populations (see van Rooijen et al., 2017). While the specific content and parameters differ between studies, they all share the general structure: a trial starts with the presentation of two stimuli for a pre-specified duration on two sides of the screen and equidistant to the centre. After they disappear, a probe appears on one of the two picture location which the participant has to react to. If the target stimulus (e.g., an emotional one) is replaced by the probe, the trial is defined as 'congruent'. In contrast, in an 'incongruent' trial, the probe appears on the location of the control stimulus (e.g., a neutral one). The attentional bias is then usually calculated by looking at a difference value between reaction times during congruent and incongruent trials.

Studies looking at attentional biases to emotional facial expressions using this task have reported attentional biases to both positive (e.g., Wirth & Wentura, 2020) and negative facial emotional expressions (e.g., Bradley et al., 1997; Carlson & Mujica-Parodi, 2015). However, when contrasting different emotion categories in the dot-probe task, some studies only found a bias towards specific emotions (e.g., Valk et al., 2015) while other studies found no bias in reaction times at all (e.g., Puls & Rothermund, 2018). Methodological differences between studies, for example, in the timing of the stimuli or the stimulus content have been suggested as potential explanations for the mixed evidence (Cooper & Langton, 2006; van Berlo et al., 2020). Importantly, inconsistent findings can also be driven by individual differences (Yiend, 2010). For example, an altered processing of emotional (facial) stimuli, including attentional processes, has been described in various mental health conditions (Kret & Ploeger, 2015).

Attention to Emotion in Social Anxiety

Being characterized by a disproportionate and impairing fear of scrutiny in social situations, Social Anxiety Disorder (SAD) is a mental health condition that already suggests altered attentional allocation to social information by definition (DSM-V; American Psychiatric Association, 2013). The most prominent cognitive-behavioural models on the development and maintenance of SAD all describe a shift in attention to the self as a social object once a social situation is entered or even anticipated (Clark & Wells, 1995; Heimberg et al., 2010, 2014; Hofmann, 2007; Rapee & Heimberg, 1997). This altered attention entails an increased awareness of negatively biased cognitive self-representations and physiological arousal. The *cognitive-behavioral model of anxiety in social phobia* (Rapee & Heimberg, 1997; updates: Heimberg et al., 2010, 2014) additionally posits that attention is tuned to external cues in order to inform mental self-representations. Facial expressions are one example of these cues which can indicate possible negative evaluations by others, which people with SAD fear. This theoretical assumption has been confirmed in various empirical studies showing altered attention to angry facial expressions, representing social threat, in socially anxious individuals (e.g., Lazarov et al., 2021). In line with this, findings from dot-probe studies overall, yet not consistently, report an attentional bias towards threat faces (for a review, see Bantin et al., 2016). Different mechanisms have been suggested to underlie biased attention to threatening stimuli, namely (a) an initial vigilance to threat which; (b) is followed by avoidance after longer exposure (Mogg, Bradley, et al., 2004), as well as; (c) a prolonged attentional capture by threat stimuli, (i.e., difficulty in disengagement; Cisler & Koster, 2010). In the dot-probe task, the difficulty to disengage from threat with higher social anxiety was predominantly found in non-clinical samples (Salemink et al., 2007), whereas a vigilance to threat was prevalent in clinical samples (Klumpp & Amir, 2009).

Importantly, even though different types of emotional expressions appear in a social context and could provide relevant (evaluative) information about other people (Heimberg et al., 2010, 2014; Rapee & Heimberg, 1997), there is only limited research on altered attentional biases toward emotional facial expressions other than anger (Mogg, Philippot, et al., 2004). In these few studies, (altered) biases, if present at all, were less pronounced compared to the anger bias. The number and breadth of these studies is, however, too limited to draw any conclusions on biased attention to emotions other than anger in social anxiety. Thus, our study aims to contribute to a better understanding of altered attention to emotional expressions associated with social anxiety by including various emotional facial expressions.

Attention to Emotion in Autism

Another clinical population that has been found to show alterations in attention to emotional facial expressions are autistic individuals. They tend to attend to faces and, specifically the eye and mouth region, less (Chita-Tegmark, 2016), which might contribute to difficulties in identifying emotions (Kliemann et al., 2010). It has been long assumed that the active avoidance of the eye region, conveying emotional information, would be driven by an unpleasant hyperactivation of the amygdala in autistic individuals (relevance detection theory; Zalla & Sperduti, 2013). Recently, however, avoidance of the eye region was claimed to be the result of preventing both hypo- and hyperarousal (two pathway model; Cuve et al., 2018). Attention to facial emotional expressions thus seems to be related to unpleasant arousal levels in autistic individuals. Yet, biased attention towards threatening faces specifically was observed in autistic children and adults (Fan et al., 2020). This led to the claim that the "anger superiority effect" (Hansen & Hansen, 1988) as basic adaptive phenomenon would be unaltered in autistic individuals (Gaigg, 2012). As an alternative explanation, given the high comorbidity between social anxiety and autism (Spain et al., 2018), the question was raised whether the threat bias observed in autistic individuals could be attributed to comorbid social anxiety. Specifically in the social domain, autistic and socially anxious individuals show similar patterns, such as choosing to be alone and avoiding or disliking social situations (White et al., 2012). Apart from one exception (Hollocks et al., 2016), experimental studies, however, have found no evidence for an influence of anxiety symptoms on the threat bias in ASD using the dot-probe task (Hollocks et al., 2013; May et al., 2015). Importantly, as most of the available dot-probe studies examine alterations in ASD, these studies were performed with a developmental sample (children/teenagers), thus limiting the generalizability of the results.

Similarly, alterations in biases to emotional expressions other than anger have mostly been investigated in autistic children. Here, one study found no evidence of a bias to happy (nor angry) facial expressions (May et al., 2015), whereas another study found no biases toward happy or sad expressions (García-Blanco et al., 2017) in both neurotypical and autistic children. The inconclusive evidence from developmental samples is also reflected in the scarce adult literature on this topic: In one study, only adults with low but not with high autistic trait levels, showed an attentional bias to fearful expressions (Miu et al., 2012). In another study, in contrast, no differences in attentional biases between autistic and non-autistic adults were found. Both groups showed attentional biases to happy and angry faces, but not to sad faces (Monk et al., 2010). Examining all existing evidence together, it is not clear whether attentional biases to specific emotional expressions exist in autistic adults. In the current study, we attempted to diminish this knowledge gap by measuring autistic trait levels and relating them to attentional biases toward various emotional expressions.

Present Study

The goal of this study was to examine whether variability in attentional biases toward different emotional facial expressions can be explained by trait levels associated with ASD and SAD in the general population. More specifically, we administered a modified version of the emotional dot-probe task on a touchscreen (see van Berlo et al., 2020) in public settings (community sample) as well as in a lab setting (student sample). To replicate as well as expand current findings on attentional biases to specific emotions, we paired angry, happy, sad, and fearful expressions with neutral expressions in the dot-probe task, and assessed autistic and social anxiety traits via self-reports. The hypotheses, including statistical models to test them, were preregistered on the Open Science Framework after data collection but before accessing the data (see https://osf.io/8pwgy for the preregistration, including a more detailed description of the hypotheses). In line with the proposed adaptive function of increased attention to emotions serving as communicative signals (Crivelli & Fridlund, 2018) as well as the results from most dot-probe studies to date (however, see Puls & Rothermund, 2018), we expected to observe an attentional bias toward all emotions. Given the high relevance of angry facial expressions as (social) threat signals, attentional biases might especially be pronounced for expressions of anger (e.g., Valk et al., 2015). We expected that variability in this bias could be explained by social anxiety traits, particularly that higher social anxiety trait levels would be associated with stronger biases. The possibility of a stronger attentional bias to other emotional expressions in individuals with higher levels of social anxiety traits was additionally explored, including the goal to contrast increased initial vigilance with a difficulty to disengage from emotional expressions. Given the inconclusive literature on the relationship between autism and attentional biases in adults, we hypothesized that, due to an avoidance of the eye region, a less pronounced bias to emotional facial expressions should become apparent with higher autistic trait levels. The bias to angry faces should, however, not be linked to autistic trait levels, as suggested by past research in clinical populations (Fan et al., 2020). Further, the comorbidity between social anxiety and autism has been discussed, yet not confirmed, as being a potential source of a threat bias in individuals with ASD (e.g., May et al., 2015). Therefore, we also aimed to explore whether the link between autistic trait levels and the attentional bias towards angry faces would depend on simultaneously heightened social anxiety trait levels (i.e., a moderation effect) in our healthy sample.

Method

Participants

We tested 104 participants (75 female) with a mean age of 31.4 years (*SD* = 14.5, Range: 17 -71) and the majority (*n* = 95) being right-handed. All participants reported to have no prior or current psychological or neural disorder and performed the experiment either in English (*n* = 14) or in Dutch (*n* = 90). Data was collected in three different settings in the Netherlands: the primate park 'Apenheul' in Apeldoorn (*n* = 30), the science festival 'Night of Discoveries' in Leiden (*n* = 22) and a laboratory at Leiden University (*n* = 52). One participant at the primate park and one participant at the science festival had incomplete task data and were disregarded from the analysis (*N* = 102). Sample characteristics for each location can be found in Table S1 in Online Resource 1. The total sample size was not predetermined as we could not predict the motivation of the primate park/science festival to participate in our study. Yet, the sample size for the laboratory setting was matched to the public settings to balance our sample. All participants provided informed consent prior to participation and there was no monetary reward in either setting but student participants could receive one course credit. The study was conducted in accordance with the Declaration of Helsinki and received approval by the local ethics committee of the Faculty of Social and Behavioural Sciences at Leiden University.

Stimuli and Task

To create our facial emotional expression stimuli, six identities (three female) displaying acted angry, happy, sad, fearful and neutral expressions were chosen from the NimStim database (Tottenham et al., 2009). The face (including the neck) of each stimulus was cut out and the remainder replaced by a grey background (RGB: 145, 145,145), matching the colour of the task background. In order to ensure that observed effects in the dot-probe task were likely to not be caused by systematic differences in low-level features between emotion categories (e.g., de Cesarei & Codispoti, 2013), we employed the Protosc toolbox (Stuit et al., 2021) to unveil potential features significantly predicting category membership. Significant features could not be found for any of the available feature spaces (Fourier magnitudes, Fourier phases, HOGs, colour distributions and pixel intensities. The dot-probe task was programmed in E-Prime 2.0 and conducted on an Iiyama T1931SR B1 touchscreen (38 x 30 cm).

A trial was initiated by tapping on a black dot (Ø 6 cm) in the centre of the screen. Immediately afterwards, two pictures appeared (each 11 x 15 cm), one on the left side (7 cm from the left edge) and one on the right side (31 cm from the left edge) of the screen. Apart from the baseline trials in which only neutral stimuli were presented, one picture contained a neutral expression and the other picture contained an emotional expression of the same identity. After 300 ms (according to the recommendation by van Rooijen et al., 2017), one of the pictures was replaced by a black dot (Ø 6 cm) which the participant had to tap on as fast as possible. In line with the existing dot-probe terminology, a trial was labelled as congruent when an emotional (i.e., target) expression was replaced by the dot, whereas the replacement of a neutral expression was regarded as an 'incongruent' trial. The participant's reaction time to this second dot was measured in each trial as the variable of interest. After participants successfully reacted to the second dot, the screen turned blank (grey) for 2 s after which the start dot of the next trial appeared (see Figure 1). For each emotion category (angry, happy, fearful, sad) paired with a neutral stimulus, the dot could appear in the congruent or incongruent location, resulting in eight potential combinations. Each of the combinations was presented using each of the six stimulus identities and with the emotional stimulus in either the left or right location. Further, participants completed 12 trials in which two neutral stimuli were shown after which, due to a coding error, the dot always replaced the left stimulus. Thus, every participant had to complete 108 trials in total (8 x 6 x 2 + 12).

Procedure

After signing the informed consent form, participants received written instructions on how to perform the dot-probe task on the touchscreen. They then completed eight practice trials with flower pictures as stimuli. Due to the self-initiation of each trial by tapping on the start dot, participants could go through the experiment in a self-paced manner and take breaks whenever necessary. After performing the task (duration around 7 min), participants completed the clinical trait questionnaires and were debriefed.

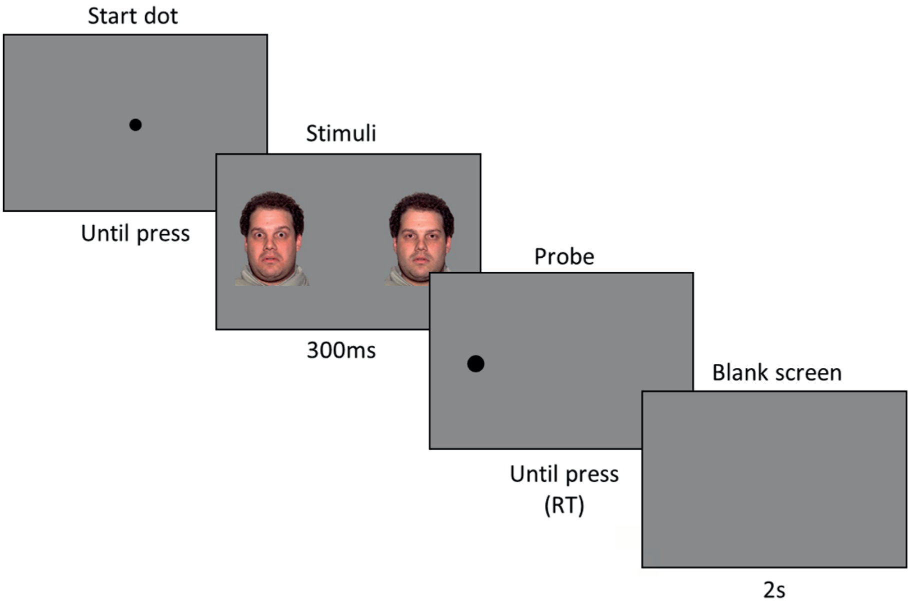


Figure 1. Structure of a trial in the dot-probe task. Participants were instructed to press the dot on the touch screen, and the reaction time (RT) to the second dot (probe) was measured. With the probe appearing behind the emotional face, the displayed trial represents a congruent trial. Stimuli were taken from the NimStim set of Facial Expressions (Tottenham et al., 2009).

Questionnaires

Social Anxiety Traits

We used the self-report version of the Liebowitz Social Anxiety Scale (LSAS; Liebowitz, 1987) to measure social anxiety traits in our healthy sample. The LSAS was originally developed to quantify fear and avoidance in individuals with social phobia and consists of 24 items describing different social situations that typically evoke performance or social anxiety. Fear and avoidance with regard to each item is rated separately on a 4-point Likert scale, ranging from 0 (fear rating: none; avoidance rating: never) to 3 (fear rating: severe; avoidance rating: usually). Sum scores across all items, including both fear and avoidance ratings, are calculated as an overall social anxiety trait measure, with potential scores ranging from 0 to 144. Given that one participant did not complete the questionnaire at all, we had data from 103 participants. Further, for six participants, single items were imputed (see Online Resource 2). Our final sample's LSAS scores (N = 101; participants without task data excluded) ranged between 4 – 83 (M = 37.1, SD = 17.2). The distribution of the LSAS scores had a skewness of 0.43 and a kurtosis of 2.81, thus being close to normal with a light right skew and mesokurtic shape. Internal consistency of the LSAS in our sample was excellent (α = .91, 95% CI [.89, .94]).

Autistic Traits

We used the Autism-Spectrum Quotient (AQ; Baron-Cohen et al., 2001) to measure variations in traits associated with Autism Spectrum Conditions in our sample. The AQ consists of 50 items associated with five different domains in which alterations are typically observed: social skill, attention switching, attention to detail, communication, and imagination. Ten items belong to each domain respectively and build one subscale of the AQ. In this questionnaire, respondents rate the degree to which items apply to them on a 4-point Likert scale, from 1 = *definitely agree* to 4 = *definitely disagree*. Some items are reverse coded and all scores are eventually transformed to binary values (1/2 to 0 and 3/4 to 1). A higher sum score of all items, potentially ranging between 0 and 50, reflects higher autistic trait levels. Three participants did not complete the AQ at all and we imputed missing items for four participants who had incomplete data (see Online Resource 2). The AQ sum scores encompassed values between 2 – 38 (M = 18.3, SD = 7.6) in our sample (N = 99; participants without task data excluded). With a skewness of 0.69 and a kurtosis of 3.33, the AQ score distribution was also close to normal, yet slightly right-skewed and platykurtic. The AQ in our sample showed a good internal consistency (α = .84, 95% CI [.79, .88]).

Data Analysis

Before fitting the models, reaction times smaller than 250 ms were excluded given that they likely represent random responses (see van Berlo et al., 2020). Further, for each participant, trials exceeding their median reaction time + 2.5 median absolute deviations were excluded to filter out trials in which participants might have been distracted, thus resulting in relatively unusual high RTs. This lead to an exclusion of 9.47 % of all trials (angry: 8.83 %, happy: 9.24 %, sad: 10.25 %, fearful: 10.02 %, neutral: 8.59 %). All analyses were performed in R 3.6.3 (R Core Team, 2020; see Online Resource 2 for further information).

Pre-registered Data Analysis

For all hypotheses, we aimed to fit multiple linear mixed models on reaction times. Looking at the model diagnostics, we did not spot major divergences from assumptions. The selection of the basic fixed and random effect structure for all models was informed by model comparisons based on the first model (see Online Resource 2). Eventually, we included random intercepts for *Subject* and *Trial* . The two three-way interactions *Age*Congruency*Emotion category* and *Sex*Congruency*Emotion category,* as well as all two-way interactions and main effects, were defined as predictors in all models.

To test our first hypothesis, namely that there is an attentional bias to emotional expressions and that this bias is specifically pronounced for angry expressions, we looked at the interaction between *Emotion category* and *Congruency* (controlled for by *Age* and *Sex*) as hypothesis-specific predictor in our model. Both factors, *Emotion category* and *Congruency*, were sum-coded in all analyses. To test our second and third hypotheses, namely that the attentional bias to emotions and specifically to threat expressions is enhanced with higher social anxiety traits, a three-way interaction between *Emotion category*, *Congruency* and *Social anxiety traits* was added as hypothesis-specific predictor to the model (including all two-way interactions).

Since we could not find a link between attentional biases and *Social anxiety traits* for any emotion, we did not explore a potential moderating effect of context in this interaction, as indicated in the preregistration[2]. Based on the same rationale, we did not conduct the second planned exploratory analysis, which aimed to disentangle whether an alteration in attentional bias would be due to heightened vigilance for emotional expressions or a stronger difficulty to disengage from emotional expressions with elevated social anxiety traits.

In order to test the presence of a general reduction in attentional bias to emotions with higher autistic levels, with the exception of angry expressions (hypotheses 5), we added a three-way interaction between *Emotion category*, *Congruency* and *Autistic traits* as hypothesis-specific predictors to the general model (including all two-way interactions). Given that, there was indeed no link between the attentional bias towards angry expressions (as to all other expressions) and *Autistic traits*, we tested for a potential moderating effect of *Social anxiety traits* on *Autistic traits* in the prediction of the bias to angry expressions. More specifically, we fitted a model on the reaction times in trials with angry expressions with a three-way

2 To confirm that the attentional bias effect was comparable in all experimental settings, we tested for a modulation of the congruency effect by the specific location (primate park, science festival and lab) as well as by the context (public [primate park + science festival], lab). Neither interaction was significant.

interaction between *Congruency*, *Social anxiety traits* and *Autistic traits,* including all two-way interactions and the control predictor terms.

Exploratory Data Analysis

As we did not observe the expected links between attentional biases and clinical trait dimension, and could not exclude that this might be due to a lack of power, we ran additional explorative data analyses, using Bayesian mixed models. Bayesian models were created in the Stan computational framework and accessed using the brms package (Bürkner, 2017, 2018), version 2.17.0. We sum coded all factorial predictors, and scaled and centered all continuous predictors. All models were run with 4 chains and 5000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation plots (Depaoli & Van de Schoot, 2017). We found no divergences or excessive autocorrelation.

For the exploratory analyses, we used the same dataset as for the pre-registered analyses in which extremely fast and slow reaction times were excluded by subject (see first paragraph of Data analysis section). However, for the exploratory analyses we rescaled our dependent variable in order to filter out the effect of handedness*probe location (*Probe distance*) and to ease setting a prior for the intercept. Thus, we centered the reaction times within *Subject* within *Probe distance* level (close vs. far). Thereby, we removed the distance effect and removed overall differences in reaction times between participants.

First, we explored attentional biases within each emotion category by creating a model with centered reaction time as dependent variable and *Congruency* and *Emotion Category* and their interaction as predictors. Furthermore, we allowed the effects of all predictors to vary by *Subject*. Second, we explored whether attentional biases within each emotion category were linked to *Autistic traits* and *Social anxiety traits* by including the interactions *Congruency*Emotion Category*Autistic traits* and *Congruency*Emotion Category*Social anxiety traits*. We used regularizing Gaussian priors with $M = 0$ and $SD = 5$ for all fixed effects, a Gaussian prior with $M = 0$ and $SD = 1$ for the intercept, and default half Student t priors with 3 degrees of freedom for the random effects and residual standard deviation. We used multiple measures to summarize the posterior distribution resulting from our models: (I) the median estimate and the median absolute deviation of this estimate, (II) the 95% credible interval, and (III) the probability of direction (pd). The 95% CrI indicates the range within which the effect falls with 95% probability, while the pd indicates the proportion of the posterior distribution that is of the median's sign (Makowski et al., 2019).

Results

Pre-registered Analyses

General Attentional Bias to Emotions

As expected, we found a significant congruency effect in the general model on the reaction times in the dot-probe task, $B = -5.79$, 95% CI [-9.80, -1.78], $t(8697.27) = -2.83$, $p = .005$ (see Figure 2A). Confirming an attentional bias to emotional expressions, participants were on average 5.79 ms faster when the dot appeared behind the emotional expression and 5.79 ms slower when the dot appeared behind the neutral expression than their average reaction times in trial with an emotion-neutral pair. There was, however, no evidence for an enhanced attentional bias to angry compared to other facial expressions, that is, no significant interaction between *Emotion category* and *Congruency*. In addition to the general congruency effect, we also observed significant effects of the included control predictor terms. Unsurprisingly, reaction times depended on *Age*, $B = 2.94$, 95% CI [1.78, 4.10], $t(98.96) = 5.04$, $p < .001$. While older participants overall reacted more slowly to the dot probe than younger participants, this effect was less marked in trials including a happy face, $B = -0.27$, 95% CI [-0.47, -0.07], $t(8708.16) = -2.70$, $p = .007$, as revealed by the significant interaction between *Age* and *Emotion category*. Lastly, *Probe distance* significantly predicted reaction times, with slower responses to far probes (i.e., a mismatch between handedness and probe location) compared to close probes (i.e., handedness and probe location matched), $B = 30.94$, 95% CI [27.62, 34.25], $t(8703.67) = 18.30$, $p < .001$. For an overview of the model fit, see Table 1 as well as Table S3 in Online Resource 1 for the coefficients of all factor levels.

Social Anxiety Traits and the Attentional Bias to Emotions

Against our hypothesis, we did not find any alteration in the overall or emotion-specific attentional bias related to social anxiety trait levels. Further, the congruency effect which we observed in the general model did not reach significance in the model including *Social anxiety traits* ($p = .166$). Yet, the effect of *Age* on reaction

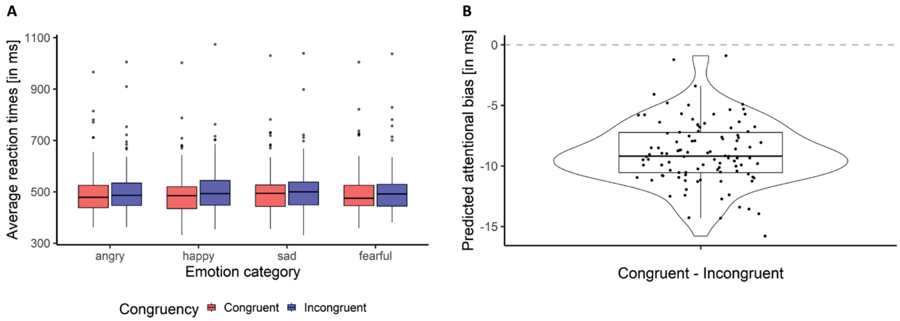


Figure 2. (A) Average reaction times per subject to the probe in congruent versus incongruent trials for each emotion category. Boxes enclose all values between the first and third quartile (Inter-quartile range, IQR) and the whiskers extend to +/- 1.5 IQR from the respective quartile. As outliers in reaction times were defined on an individual basis, outliers in this plot represent subjects with slow reaction times on average (see also Table S2 in the Supplementary Materials). (B) Mean predicted attentional bias (difference in reaction times between congruent and incongruent trials) per subject across emotion categories and trials. The data distribution is visualized by the violin as well as by the box (same definition as above), and single data points represent subjects. This graph shows the significant congruency effect, i.e., the general bias towards emotional facial expressions.

times to the dot probe was again significant, $B = 3.01$, 95% CI [1.83, 4.20], $t(96.96) = 5.05$, $p < .001$, as well as the interaction between *Age* and *Emotion category*. The slowing in reaction time with higher age was less pronounced if a happy facial expression (compared to the other emotions) was included in the emotion-neutral pair, independent of the probe position, $B = -0.28$, 95% CI [-0.48, -0.08], $t(8617.1) = -2.78$, $p = .005$. As observed in the general model, a far *Probe distance* was associated with slower reaction times, $B = 30.81$, 95% CI [27.50, 34.13], $t(8613.15) = 18.20$, $p < .001$. Table 2 provides an overview of the model fit and Table S4 in Online Resource 1 describes all coefficients.

Autistic Traits and the Attentional Bias to Emotions

In the attentional bias model including *Autistic traits*, there was a significant interaction between *Autistic traits* and *Emotion category*. More specifically, responses after emotion-neutral pairs with an angry facial expression were faster with higher autistic traits, $B = -0.62$, 95% CI [-1.00, -0.24], $t(8444.09) = -3.22$, $p = .001$. In contrast, emotion-neutral pairs with sad facial expressions were related to slower responses with higher autistic traits, $B = 0.39$, 95% CI [0.01, 0.78], $t(8443.17) = 2.03$, $p = .042$. Importantly, these effects were independent of the probe location (i.e., *Congruency*) and we did not observe the expected link between the attentional bias and *Autistic traits*. Further, a closer examination of the effects revealed that none of the slopes were significantly different from zero. In line with the general model on the attentional bias to emotions, *Congruency*, B = -7.48, 95% CI [-13.06, -1.90], t(8439.91) = -2.63, p = 0.009, as well as the control terms *Probe distance*, B = 30.11, 95% CI [26.81, 33.41], t(8439.65) = 17.90, p < .001, and *Age*, B = 3.12, 95% CI [1.87, 4.37], t(94.96) = 4.97, p < 0.001, were significant predictors of reaction times in the model including *Autistic traits*. Participants reacted faster in congruent trials, as well as when the probe appeared on the side of their dominant hand and when they were younger. We also found a significant interaction between *Emotion category* and *Age*. Here, the slowing in reaction times with higher age was more pronounced in trials with angry facial expressions, B = 0.24, 95% CI [0.03, 0.44], t(8446.75) = 2.23, p = .026, and less pronounced in trials with happy facial expressions, B = -0.32, 95% CI [-0.52, -0.11], t(8432.03) = -3.01, p = .003. A summary of the model fit can be found in Table 2 and a closer description of all coefficients in Table S5 in Online Resource 1.

Autistic Traits, Social Anxiety Traits and the Attentional Bias to Angry Facial Expressions

In line with previous research, the two questionnaire scores, indicating autistic trait and social anxiety traits, were significantly positively correlated in our sample, r_s = .30, p < .001. Zooming in on a potential moderating effect of *Social anxiety traits* on the link between *Autistic traits* and the attentional bias to angry facial expressions, our model revealed a significant three-way interaction between *Congruency*, *Social anxiety traits* and *Autistic traits*, B = 0.03, 95% CI [0.01, 0.06], t(2056.63) = 2.52, p = .012. An examination of the predicted value plots (see Figure 3) as well as slope comparisons (see Table 3) at three different values on one of the trait dimensions (mean – 1*SD*, mean, mean + 1*SD*) suggested that this interaction is likely to be driven by a decrease in attentional bias with higher autistic traits at a relatively "high" social anxiety trait level (mean + 1*SD*) and/or an increase in attentional bias with higher social anxiety traits at a relatively "low" autistic trait level (mean – 1*SD*). In the context of this three-way interaction, the two-way interactions between each trait dimension and *Congruency* were also approaching significance (see Table 2). However, when running the same model without the three-way interaction added, this was not the case. Similar to the previous models with multiple emotion categories, *Congruency*, B = 23.36, 95% CI [1.01, 45.72], t(2056.92) = 2.05, p = .041 , as well as the control predictors *Age*, B = 3.48, 95% CI [2.19, 4.78], t(92.90) = 5.33, p < .001, and *Probe distance*, B = 36.69, 95% CI [29.94, 43.44], t(2056.97) = 10.66, p < .001, were significant predictors in this model (see Table 2 for an overview of the model fit as well as Table S6 in Online Resource 1 for all coefficients).

Table 1 Results of the Linear Mixed-Effects Models Predicting Reaction Times to the Dot Probe. Output for the Fixed and Random Effect Terms for the Model without Clinical Traits and its Interactions as Predictor, as well as for the Models with Social Anxiety Traits and Autistic Traits, Respectively, are Shown.

	General model				**Social anxiety traits model**				**Autistic traits model**			
Fixed effects	*df1*	*df2*	*F*	*p*	*df1*	*df2*	*F*	*p*	*df1*	*df2*	*F*	*p*
Emotion category	3	8705.6	1.44	.230	3	8620.7	1.50	.212	3	8441.7	1.01	.389
Congruency	1	8697.3	8.03	**.005**	1	8624.9	1.92	.166	1	8441.7	6.91	**.009**
Age	1	99.0	25.41	**< .001**	1	97.0	25.47	**< .001**	1	95.0	24.69	**< .001**
Gender	1	99.0	0.16	.687	1	97.0	0.03	.867	1	95.0	0.21	.645
Probe distance	1	8703.7	334.82	**< .001**	1	8613.2	331.29	**< .001**	1	8439.7	320.41	**< .001**
Clinical traits					1	97.0	0.56	.456	1	95.0	0.19	.665
Emotion category*Congruency	3	8696.1	0.96	.412	3	8607.1	0.46	.707	3	8435.2	0.75	.524
Emotion category*Age	3	8711.9	2.68	**.045**	3	8620.3	2.98	**.030**	3	8443.0	3.66	**.012**
Congruency*Age	1	8704.0	0.91	.339	1	8617.6	0.74	**.388**	1	8438.8	0.55	.458
Emotion category*Gender	3	8708.1	0.36	.780	3	8617.6	0.36	.781	3	8440.7	0.51	.674
Congruency*Gender	1	8712.0	0.97	.325	1	8618.9	1.37	.242	1	8441.6	1.08	.298
Emotion category*Clinical traits					3	8624.8	0.86	.462	3	8445.5	3.92	**.008**
Congruency*Clinical traits					1	8624.7	0.31	.578	1	8454.6	1.04	.308
Emotion category*Congruency*Age	3	8693.2	1.17	.321	3	8601.1	1.02	.382	3	8427.5	0.70	.551
Emotion category*Congruency*Gender	3	8704.0	0.40	.754	3	8611.4	0.49	.689	3	8437.1	0.33	.801
Emotion category*Congruency*Clinical traits					3	8613.3	1.02	.381	3	8441.6	0.19	.905
Random effects	**Variance**				**Variance**				**Variance**			
Intercepts	Subject				Subject				Subject			
	N = 102			7045.49	*N* = 101			7112.70	*N* = 99			7161.27
	Trial				Trial				Trial			
	N = 108			52.37	*N* = 108			49.74	*N* = 108			57.10
Residual variance				6267.42				6221.84				6016.66

Note. df1 = numerator degrees of freedom; df2 = denominator degrees of freedom.

Table 2. *Results of the linear mixed-effects models predicting reaction times to the dot probe in trials with angry facial expressions.*

Fixed effects		***df1***	***df2***	***F***	***p***
Congruency		1	2056.91	4.20	**.041**
Age		1	92.90	28.44	**< .001**
Sex		1	92.81	0.06	.813
Probe distance		1	2056.97	113.60	**< .001**
Autistic traits		1	92.89	0.01	.921
Social anxiety traits		1	93.07	1.44	.233
Congruency*Age		1	2056.57	0.50	.479
Congruency*Sex		1	2056.53	0.09	.768
Congruency*Autistic traits		1	2056.69	3.86	**.050**
Congruency*Social anxiety traits		1	2056.71	7.51	**.006**
Autistic traits*Social anxiety traits		1	93.09	0.63	.428
Congruency*Autistic traits*Social anxiety traits		1	2056.63	6.37	**.012**
Random effects					**Variance**
Intercepts	Subject *N* = 99				7204.31
Residual variance					6362.83

Note. Df1 = numerator degrees of freedom; df2 = denominator degrees of freedom.

Table 3. Difference in the slopes between congruent and incongruent trials (congruency effect) with higher levels on one clinical trait dimension at the trait scores mean -1SD, mean and mean +1SD on the respective other clinical trait dimension

	Slope difference : congruent – incongruent [SE]	**95% CI**	**df**	***t***	**p-value**
Autistic traits					
Mean LSAS – 1SD [19.96]	-0.82 [0.67]	-2.13, 0.48	2057	-1.24	.216
Mean LSAS [37.26]	0.32 [0.49]	-0.65, 1.28	2056	0.64	.520
Mean LSAS + 1SD [54.57]	1.46 [0.67]	0.15, 2.77	2056	2.18	**.030**
Social anxiety traits					
Mean AQ – 1SD [10.64]	-0.87 [0.34]	-1.53, -0.21	2057	-2.58	**.010**
Mean AQ [18.18]	-0.37 [0.23]	-0.83, 0.09	2057	-1.59	.112
Mean AQ + 1SD [25.73]	0.13 [0.27]	-0.40, 0.66	2057	0.47	.638

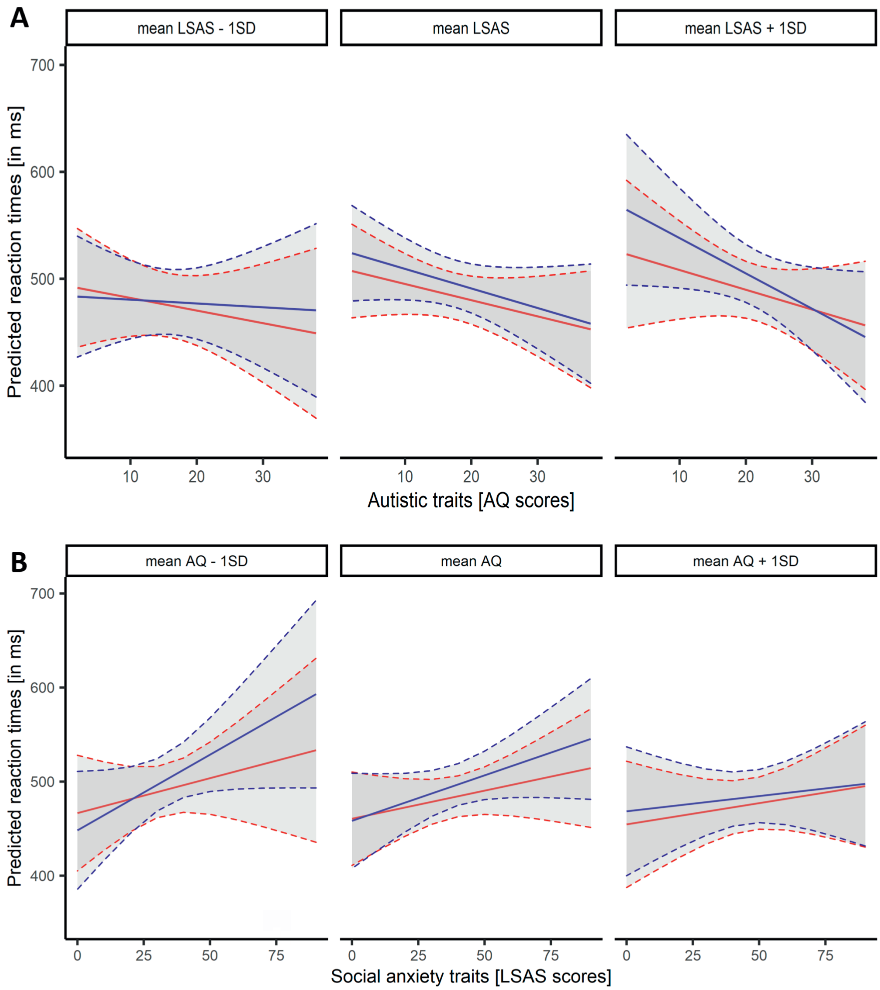


Figure 3. Effects of levels on one trait dimension on reaction times at distinct levels on the other trait dimension in congruent (red) vs. incongruent (blue) trials. Effects are displayed at the mean -1SD, mean and mean +1SD of the other trait dimension respectively.

Exploratory Analyses

First, we explored whether participants showed attentional biases within each emotion category using a Bayesian mixed model (Table S7 in Online Resource 1). We found clear effects of *Congruency* within each level of *Emotion category* (Figure S1 in Online Resource 1), with participants responding faster on trials where the probe replaced the emotional stimulus versus neutral stimulus (Angry: -9.21 ms [3.39], 95% CrI [-15.86, -2.31], *pd* = 1.00; Happy: -13.30ms [3.27], 95% CrI [-19.59,

-6.98], *pd* = 1.00; Sad: -6.37 ms [3.13], 95% CrI [-12.57, -0.13], *pd* = .98; Fearful: -6.65 ms [3.38], 95% CrI [-13.34, 0.02], *pd* = .98). Note that the 95% CrI for Fearful spans just over zero. However, the directionality of the effect (*pd*) was clear and consistent with the other categories.

Next, we explored whether *Autistic traits* and *Social anxiety traits* moderated the effect of *Congruency* within each level of *Emotion Category* (Table S8 in Online Resource 1). We compared the effect of *Congruency* at −1*SD* with +1*SD* of the scaled *Autistic traits* and *Social anxiety traits* variables. With regard to *Autistic traits,* we did not find robust evidence that autistic trait levels moderated the effect of *Congruency* within any level of *Emotion category* (Figure 4A; Table 6). However, we observed that participants with low autistic trait levels had a stronger attentional bias for happy faces than participants with high autistic trait levels. Although the 95% CrI spanned over 0, the directionality of the effect was clear (*pd* = .94). Looking at *Social anxiety traits,* we did not find robust evidence for an effect on *Congruency* (Figure 4B; Table 4). Even though the results indicated that people who scored higher on the social anxiety trait scale had stronger attention biases for sad, happy and angry expressions, the 95% CrIs spanned over 0, and the directionalities were relatively low (Table 4).

Table 4. Difference in the congruency effect at between −1SD and +1SD of the AQ scale (Autistic traits) and LSAS scale (Social anxiety traits) for each emotion category.

	Median [MAD]	**95% CrI**	***pd***
Autistic traits (AQ)			
Angry	4.57 [7.32]	-9.71, 19.41	.74
Happy	10.12 [6.74]	-3.00, 23.61	.94
Sad	5.28 [6.93]	-8.13, 18.71	.78
Fearful	0.28 [7.18]	-14.03, 14.47	.52
Social anxiety traits (LSAS)			
Angry	-6.49 [7.19]	-20.80, 8.01	.81
Happy	-7.58 [6.87]	-20.97, 5.71	.87
Sad	-6.40 [6.78]	-19.82, 7.14	.83
Fearful	7.27 [7.28]	-7.15, 21.26	.84

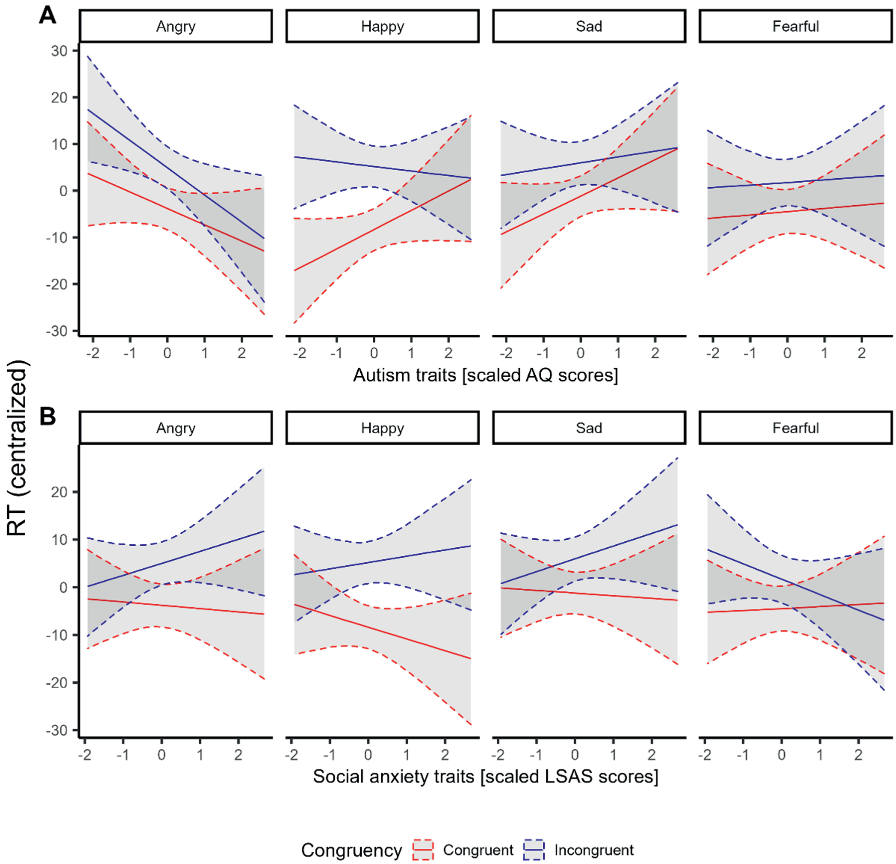


Figure 4. Effect of the interactions between congruency and social anxiety traits (LSAS) and congruency and autistic traits (AQ) on reaction times. Shaded areas reflect 95% credible intervals

Discussion

In the current study, we examined attentional biases toward facial emotional expressions and their association with autistic traits and social anxiety in a general population sample. In line with most previous research, we observed attentional biases toward various emotional facial expressions, using both frequentist as well as Bayesian analysis approaches. In contrast to our hypothesis and a vast amount of literature, higher social anxiety trait levels were overall not associated with a stronger bias to angry facial expressions (i.e., social threat). There was also only an indication of a decreased attention to emotional expressions with higher autistic trait levels for happy facial expressions within our exploratory Bayesian analysis. Yet, independent of the probe location (congruent vs. incongruent), reaction times were faster with higher autistic trait levels for trials displaying an angry face, while they were slower for trials displaying a sad face. When zooming in on the attentional bias towards angry facial expressions, we found a significant interaction between autistic trait levels, social anxiety trait levels and congruency. This suggests that the link between the attentional bias to threat and the two trait dimensions might be more complex and require further exploration.

Social Anxiety and the Attentional Bias to Emotion

Surprisingly, an enhanced attentional bias to angry facial expression was not observed in people with higher levels of trait social anxiety. Possibly, the absence of this effect can be the result of the stimulus presentation duration that we employed in this study. According to a meta-analysis examining the link between social anxiety and the threat bias (Bantin et al., 2016a), shorter stimulus durations (< 200 ms) were associated with stronger biases. Nevertheless, attentional biases toward angry facial expressions could still be found at 500 ms and 600 ms presentation duration. Further, higher levels of social anxiety have not consistently been linked to stronger attentional biases toward angry facial expressions (Bantin et al., 2016a). A recent study in a healthy student sample reported that the half of individuals with higher social anxiety trait levels were found to have the lowest attentional bias whereas the other half was partially showing vigilance toward and partially avoidance of angry faces (Neophytou & Panayiotou, 2022). Crucially, even biases on the individual level were shown to be invariant, meaning that they change over time, and to depend on the assessment tool (MacLeod et al., 2019). The present study was the first to use a touchscreen to examine the association between social anxiety and the threat bias . Given the instability of attentional biases as well as , an interplay between various factors could explain not finding the expected effect.

When comparing the effect of social anxiety traits on the threat bias at different autistic trait levels (three-way interaction), the attentional bias only seemed to be stronger with higher social anxiety traits at low autistic trait levels. This suggests that attentional biases in social anxiety might highly depend on additional individual characteristics. As a consequence, interventions focusing on treating maladaptive attentional biases, such as Attentional Bias Modification (ABM) training (MacLeod et al., 2002), might not be beneficial for every individual. Accordingly, ABM trainings have been reported to neither consistently nor robustly result in a modification of the attentional bias toward threat (van Bockstaele & Bögels, 2014). Further, one study which found a small reduction in the bias in the visual dot-probe after ABM training, also showed that this bias is not generalizable to other tasks measuring attention to threat (van Bockstaele et al., 2017). Acknowledging the specificity of this effect, the dot-probe paradigm might not be the ideal candidate on which to directly base clinical interventions. Instead, it can be regarded as a useful additional descriptor in the complex relationship between social anxiety and the attention to emotional facial expressions.

Autistic Traits and the Attentional Bias to Emotion

We expected to observe a weaker attentional bias to all emotion facial expressions, apart from anger, with higher autistic trait levels due to a decreased processing of emotional information from the faces. In contrast to our expectations, there was only an indication of this effect for happy facial expressions in our exploratory analysis. Past research in autistic children (García-Blanco et al., 2017; May et al., 2015) as well as autistic adults (Monk et al., 2010) has found no evidence for alterations of the attentional bias to happy facial expressions. Next to the essential difference of examining a clinical population, these studies also used longer presentation times (i.e., 500 ms and/or 1500 ms) which could have allowed for a more elaborate (and less automatic) processing of the stimuli. As an alternative to arousal-related explanations (e.g., Cuve et al., 2018; Zalla & Sperduti, 2013), alterations in face processing in autistic individuals were suggested to result from "deficits" in processing social rewards, such as faces (G. Dawson et al., 2005). Studies displaying happy facial expressions directed towards the participant, as used in our study, indeed suggest that those faces are associated with lower reward values in autistic individuals compared to neurotypical individuals (Dubey et al., 2015). A recent meta-analysis, however, has challenged the idea of altered social reward processing in ASD by unveiling less reward processing for both social and non-social stimuli (Bottini, 2018). In our study, we did not investigate mechanisms which could underlie a weaker attentional bias toward happy facial expressions with higher autistic trait levels. To get a better understanding of altered face perception in ASD, future studies should not only examine whether a weaker attentional bias towards happy facial expressions is present in autistic individuals, but also what the underlying mechanism of this alteration might be.

Unexpectedly, reaction times to the dot probe in trials with angry or sad facial expressions were systematically linked to autistic traits, independent of whether the probe appeared behind the emotional or the neutral expression (i.e., congruency). Higher autistic trait levels were associated with relatively faster reaction times after the presentation of an angry face and with slower reaction times after the presentation of a sad face. A potential explanation of this finding could be that the mere presence of the expressions affected the observer's arousal more strongly with higher autistic trait levels. More specifically, independent of their location, angry expressions could have elicited increases in arousal and sad expressions decreases in arousal, which would result in faster and slower reaction times, respectively. Yet, differences in reaction times between emotion categories in the general model could not be found. Further, the slopes for the links between autistic traits and reaction times in trials with angry and sad facial expressions were not significantly different from zero. Thus, the reaction times for angry and sad expressions were only different compared to the average link between reaction times to all expressions and autistic traits.

Finally, we observed a significant interaction between social anxiety traits and autistic traits in predicting the attentional bias to angry faces. Individuals with higher autistic traits showed a reduced attentional bias towards angry faces, but only when social anxiety trait levels were also high. This was in contrast to our expectations. We assumed that high social anxiety levels would go along with a stronger attentional bias to angry faces in individuals with higher autistic trait levels, as angry expression might be perceived as more threatening. Looking at the predicted value plots, the reduced attentional bias seemed to be driven by faster reaction times to the probe in incongruent trials (i.e., probe replaces neutral faces) with higher autistic traits. This potentially supports the idea of a generally heightened arousal for angry expressions. Nevertheless, given the complexity of explaining this three-way interaction, the high overlap of confidence intervals and the lacking support of previous literature in clinical populations (Hollocks et al., 2013; May et al., 2015; Monk et al., 2010), future research should examine the interplay between autistic and social anxiety traits on attentional biases to emotion.

Limitations & Future Directions

While some previous research did not report an attentional bias toward (certain) emotional facial expressions (Puls & Rothermund, 2018; Valk et al., 2015), we found an attentional bias toward emotions for all emotion categories. This bias did not differ significantly between the expressions and ranged around 10 ms (6.37 ms – 13.30 ms) which is comparable with previous research (e.g., Monk et al., 2010). Thus, emotional facial expressions seem to automatically receive prioritised attention, highlighting their suggested communicative function as salient signals for conspecifics. Yet, caution has to be taken in the interpretation of results on attentional biases, as their appearance/significance might depend on various additional factors. One important factor that has been raised in the debate on the validity of attentional biases is the impact of low-level features (e.g., de Cesarei & Codispoti, 2013). Differences between stimulus categories regarding features such as spatial frequency are a general problem in interpreting results from dot-probe studies. We did not control our stimuli for these features to keep them as natural as possible and therefore cannot exclude this as a potential influence. Nevertheless, we compared our emotion categories with regard to specific low-level features (Stuit et al., 2021, see Methods section) and could not identify any significant differences. While there were no systematic differences between emotion categories, this comparison does not rule out the existence of differences in, for example, spatial frequency or colour distribution between distinct stimuli, which might have added noise to the data. Future studies investigating attentional processes in the field of emotion should try to account for those.

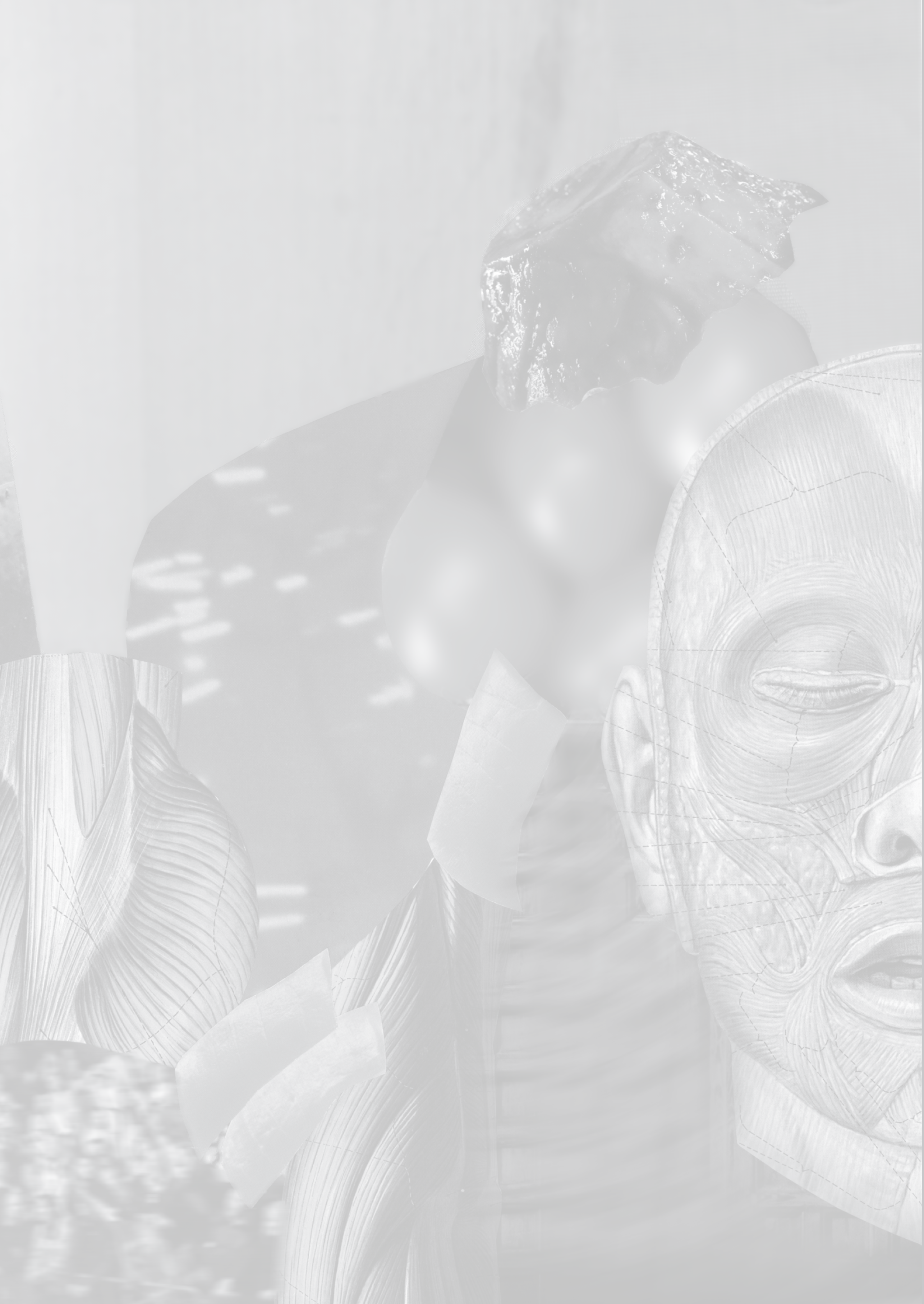
Another limitation of our study is that we did not collect data in clinical populations and could, therefore, only investigate the influence of trait levels associated with ASD and SAD on attentional biases. This complicates the direct comparison to previous research with clinical samples as well as the formulations of potential implications for clinical practice. Yet, the view of a "continuum of impairment" has become more popular regarding both social anxiety (Rapee & Spence, 2004) and autism (Robinson et al., 2011), with disorders lying on the extremes of clinical traits in the general population. While clinical relevance of symptoms is eventually determined by difficulties in daily life, alterations in information processing, as well as their underlying mechanisms, may not be qualitatively different along the trait dimension. Thus, our findings in heightened trait levels may also be informative for clinical populations.

As highlighted earlier, the link between social anxiety trait levels and attentional biases to social threat seems to depend on additional individual characteristics, such as autistic traits. This indicates that the extent to which different individuals with SAD shift their attention to external evaluative cues in social situations might also vary. Socially anxious individuals who automatically shift their attention to expressions of others might indeed benefit from trainings which aim at modifying this automatic shift to prevent the perception of social threat. In socially anxious individuals who do not show disproportionate attentional biases toward external cues, other factors might contribute more strongly to the maintenance of the disorder. While this still has to be investigated further, our results generally favour a more individualized approach, which targets specific maintenance factors in the treatment of SAD (for suggestions, see Hofmann, 2007). Since we did not find evidence for a reduced attentional bias toward emotional expressions with higher autistic trait levels, difficulties in identifying others' emotions might likely not arise from altered allocation of early visual attention (300 ms in our study) toward those. Other factors might play a more important role, such as altered physiological arousal in the presence of emotional expressions, which could also explain the earlier-mentioned effects on reaction times in our study. Future studies should specifically explore these factors, as well as their link to real-life social outcomes, to inform clinical practice.

Finally, ways of capturing attentional biases more validly have recently been suggested, such as investigating trial-level attentional biases (Zvielli et al., 2015) or using response-based measures (Evans & Britton, 2018). The use of eye-tracking as an alternative technique in examining attention towards emotional versus neutral stimuli has further been encouraged to unveil individual differences in attentional processes at different stages of information processing (Clauss et al., 2022).

Conclusion

With the current study, we aimed to unveil specific links between variations in the attentional bias to emotional facial expressions and social anxiety and autistic trait levels. While an attentional bias towards all emotional facial expressions, namely angry, happy, sad and fearful, was found in our study, there was only weak evidence for systematic links between these biases and clinical traits. More specifically, our exploratory analyses suggested that only the attentional bias to happy facial expressions was decreased with higher autistic trait levels. We did, however, additionally observe general alterations in reaction times after the presentation of certain emotional stimuli (angry, sad) with higher autistic trait levels, and the bias to angry facial expressions seemed to depend on a combination of both autistic traits and social anxiety traits in our study. Taken together, the link between clinical traits and attention, as measured by reaction times in this study, appears to be highly complex. While the dot-probe task allows to tap into general attentional tendencies toward emotional expressions, more naturalistic scenarios might be of higher informative value for revealing biases in real-life attentional processing associated with clinical conditions and build a stronger basis for clinical support.



Chapter 3

Reading your emotions in my physiology? Reliable emotion interpretations in absence of a robust physiological resonance

Abstract

Affective states are expressed in an individual's physical appearance, ranging from facial expressions and body postures, to indicators of physiological arousal (e.g. a blush). Confirming the claimed communicative function of these markers, humans are capable of distinguishing between a variety of discrete emotion displays. In an attempt to explain the underlying mechanism, characteristic bodily changes within the observer including physiological arousal and mimicry have been suggested to facilitate the interpretation of an expression. The current study aims to create a holistic picture of emotion perception by (1) using three different sources of emotional information (prototypical facial expressions, bodily expressions and subtle facial cues) and (2) measuring changes in multiple physiological signals (facial electromyography, skin conductance level, skin temperature and pupil size). While participants clearly discriminated between perceived emotional expressions, there was no overall 1-1 correspondence with their physiological responses. Some specific but robust effects were observed. Angry facial expressions were consistently responded to with a peak in skin conductance level. Further, sad body expressions were associated with a drop in skin temperature. In addition to being the best recognized expression, viewing happy faces elicited congruent facial muscle responses, which supports the potential role of embodied simulation in emotion recognition. Lastly, tears were not only rated as highly emotional intense but also evoked a peak in skin conductance in the observer. The absence of distinct physiological responses to other expressions could be explained by the lacking functionality of affect sharing in a non-interactive experimental context. Consequentially, emotional alignment in body and mind might especially take place in real social situations, which should be considered in future research.

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Data availability statement:
The datasets and materials generated and/or analysed during the current study are available on Dataverse NL: https://doi.org/10.34894/3GLSJH

Supplementary material:

Online Resource 1 | Online Resource 2 | Online Resource 3 | Online Resource 4

Humans are highly responsive to others' displays of emotions. While these can differ in form, content and context, they share the potential to resonate in the observer's body: For example, one's heart starts beating faster when seeing a person blush during a talk, one's eyes get wet when watching a grieving person in the movies and even a smiling face in an ad can make the observer mirror the expression. From a functional perspective, physiological changes in the context of emotion perception have been suggested to assist the identification of the observed person's affective state (Niedenthal, 2007; Prochazkova & Kret, 2017). In the current study, we aim to shed light on the perception of discrete emotional expressions from the face and body, subtle emotion cues, and their corresponding physiological dynamics.

Non-verbal communication of emotion with conspecifics is a shared mechanism among social animals to sustain life in groups (Y. Kim & Kret, 2022; Kret et al., 2020). Communicating emotional states can have direct survival benefits: For example, signalling disgust when faced with rotten food or displaying fear when a predator is approaching can inform conspecifics to adjust their behaviour (Curtis et al., 2011; Marsh et al., 2005; Seidel et al., 2010). In the long run, understanding and responding to emotions of group members can strengthen social bonds (A. H. Fischer & Manstead, 2016; Keltner & Haidt, 1999; Palagi et al., 2020). While leading research on emotion displays in humans has focused on prototypical facial expressions (Ekman, 1992, 1993; Ekman et al., 1980), the repertoire of nonverbal emotion signals is a lot broader in real life: Not only the face but the entire body is critically involved in communicating affect, via posture, movements, or gestures (Dael et al., 2012; de Gelder, 2009; Witkower & Tracy, 2019). On top of that, changes in physiological arousal can be reflected on an individual's face such as a blush or dilated pupils. These 'emotional byproducts' can provide additional cues to the observer (Kret, 2015; Levenson, 2003; Shariff & Tracy, 2011). To date, we are still limited in our knowledge about how different types of expressions are processed and perceived (e.g., Crivelli et al., 2016; Kret & Straffon, 2018).

Concertedly with central nervous system processes, physiological responses, i.e. (de-) activations of the peripheral nervous system, accompany and might even inform the emotional experience elicited in observers. For example, changes in facial muscle activity associated with distinct affective states (S. L. Brown & Schwartz, 1980; Ekman & Rosenberg, 2005) have frequently been described during viewing of images with prototypical emotional facial expressions (Bornemann et al., 2012; Rymarczyk et al., 2011; Varcin et al., 2019). Further, increases in sympathetic arousal as indexed by changes in electrodermal activity (e.g., Banks et al., 2012; Tsunoda et al., 2008; Vrana & Gross, 2004) or pupil dilation (Burley et al., 2017; Jessen et al., 2016; Kret, Stekelenburg, et al., 2013) have been observed when participants were shown different prototypical facial emotion displays. In contrast to specific facial muscle activations, however, changes in these markers of sympathetic activity have been suggested to arise from perceiving highly emotionally arousing stimuli in general, independent of the affective content (M. M. Bradley et al., 2008, 2017). Activation of the parasympathetic branch of the autonomic nervous system (ANS), resulting in an initial decrease in heart rate (reflecting a freezing response), has specifically been described when being exposed to expressions of anger (Dimberg, 1982; Noordewier et al., 2020; Roelofs et al., 2010). While these findings support the general idea that perceived emotional expressions resonate within the observer's body, only little is known about the generalizability of effects over expression modalities and over physiological channels since those are rarely directly compared (however see Alpers et al., 2011; Kret et al., 2013). Using multiple physiological measures, the current study explores the specificity of bodily responses when perceiving prototypical facial expressions of emotion, bodily expressions of emotion, and subtle emotion cues.

In line with influential emotion theories that highlight bodily states as constitutive parts of affect, such as the James-Lange Theory of Emotion (James, 1884; Lange, 1912) or the Somatic marker hypothesis (Damasio, 1996), researchers have tried to identify patterns in ANS activity for the experience of distinct emotional states (Friedman, 2010). Although physiological information might not be sufficient for a precise classification (Siegel et al., 2018), integrated signals from multiple bodily systems as well as predictions about one's affective state have been proposed to inform subjective emotional experience (Garfinkel & Critchley, 2013; Pace-Schott et al., 2019). But how does this relate to cases in which our own body becomes a platform to reflect other individuals' emotions on? Spontaneous mimicry of emotional expressions has not only been suggested to influence the emotional experience of the mimicker (E. Hatfield et al., 1993; Prochazkova & Kret, 2017), but also to facilitate recognition of the mimicked individual's emotions (Niedenthal, 2007; Palagi et al., 2020). The role of mimicry in emotion recognition is, to date, mostly investigated in facial muscle activity and evidence for a supporting role is mixed (against: Blairy et al., 1999; Hess & Blairy, 2001; for: Sato et al., 2013; meta-analysis: Holland et al., 2020). Importantly, physiological responses to another person's emotional expression can go beyond facial mimicry (Prochazkova & Kret, 2017) and access to a variety of signals and their integration might be crucial to facilitate emotion recognition.

The current study investigates how perceiving emotional expressions, varying in display modality and content, affects the observer's interpretation and physiology: we (1) measured multiple bodily signals while participants were presented with prototypical facial and bodily expressions of emotion as well as with subtle facial emotion cues and (2) asked participants to report how they interpreted the emotion and how intensely they perceived it. Without having a priori hypotheses about the interplay between the different variables, this approach allowed us to explore the possibility of distinct bodily responses to different emotional expressions and to evaluate their subjective interpretations, thus gaining insight in emotion processing on multiple levels.

Method

Participants

In total, 71 students from Leiden University, the Netherlands, participated in the experiment (42 female, $M_{age} = 23.36$, $SD = 3.22$, Range: 19 – 34 years-old). Inclusion criteria were normal or corrected-to-normal vision, no regular use of medication or other substances and no prior psychiatric or neuropsychological disorders. Informed consent was provided prior to participation and participants were reimbursed with either 3 course credits or 10.5€. The experimental procedures were in accordance with the Declaration of Helsinki and the study was reviewed and approved by the Psychology Ethics Committee of Leiden University (CEP18-1029/406; November 2018). Out of the 71 subjects we tested, there were technical problems for three subjects with regard to facial electromyography, skin conductance and skin temperature recordings and, for three different subjects, pupil size was not measured during the experiment (both N = 68).

Stimuli

Pictures for the three different expression modalities, namely face, body and subtle cues, were taken from existing stimulus databases and edited in Adobe Photoshop (version CC). For the prototypical facial expressions, we selected pictures of 8 identities from the NimStim set of Facial Expressions (Tottenham et al., 2009), displaying happy, angry, sad, fearful and neutral expressions respectively (40 stimuli in total; overall recognition rate in validation studies: M = 82.14% and SD = 5.42%). The bodily expressions were taken from the bodily expressive action stimulus test (BEAST; de Gelder & Van den Stock, 2011) and, similarly, our set encompassed 8 identities displaying happy, angry, sad, fearful and neutral postures each (40 stimuli in total; overall recognition rate in validation studies: M = 94.93% and SD = 2.29%). The backgrounds of the facial and bodily stimuli were cut out and replaced with a uniform grey background (RGB: 145, 145, 145). In addition, grey-scale versions of all body stimuli were created in order to control for effects of clothing colour, and a Gaussian blur was applied to their faces to control for facial expressions. In addition, three subtle facial cue stimuli (blush, dilated pupils and tears) were created by manipulating the neutral expression of each of the eight identities resulting in 24 subtle cue stimuli (for an example, see Fig. 1A). For the stimuli with dilated pupils , the original pupil size in each picture was increased to be clearly visible, on average by 23%. The 'tears' stimuli were made by artificially adding a tear on the actor's left cheek, increasing the redness of the sclera by making the veins more visible, and adding a reflection and watery blur to the eyes. Lastly, 'blush' stimuli were created by increasing the redness of the cheek region. In total, there were 104 stimuli.

Procedure

After participants provided informed consent, physiological data acquisition tools were applied, starting with electrodes for skin conductance level (SCL), then electrodes for facial electromyography (EMG) and lastly a skin temperature (SKT) sensor (for more details, see measurements section). In order to allow the signals to reach a stable baseline, a rest period of approximately 10 minutes passed before starting the data collection. In total, participants had to perform three tasks: a passive viewing task (PVT), an emotion labelling task (ELT) and an emotional dot-probe task, of which only the first two will be discussed in the scope of this paper. During both the PVT and the ELT, eye-tracking data was recorded (see measurements section) and a chin rest was used to ensure a stable head position.

The tasks were presented using Eprime 2.0 on a Dell S2240Tb 21.5 inches touch screen (1920x1080 resolution, 60 Hz refresh rate). The background colour of all screens (fixation, stimulus, blank) was set to grey (145,145,145). All participants first completed the PVT, thus allowing us to measure the initial response to the emotional expressions without a secondary task. Each trial started with the presentation of a fixation cross for 500ms, which was followed by a 4000ms presentation of one of the above described stimuli (460x510 pixels). The stimulus presentations were separated by a 3500ms, 4000ms or 4500ms blank screen to the next trial (inter-trial interval duration varied between participants). Due to a coding error, a fearful face instead of a face with added tears was presented for one of the 8 stimulus identities and had to be excluded from data analysis (7 instead of 8 trials for this stimulus category). Apart from that, each of the remaining 102 stimuli was presented once, in a randomized order. After taking a short break, participants continued the experiment with the ELT. Each trial started with a fixation cross lasting 500ms and followed by one of the expressions for 1s. Afterwards, a question appeared next to the stimulus, asking participants to indicate which of the 5 expression categories, namely angry, happy, scared (in the following referred to as 'fearful'), sad or neutral was displayed in the picture. In a second step, they had to rate how emotionally intense they perceived the stimulus, using a slider from neutral to very emotional (on a scale 0-100). There were not time constraints on the ratings and each expression was rated twice (208 trials; see Fig. 2b for a visualization of the tasks). The eyetracking recording was stopped and all electrodes were de-attached for the subsequent emotional dotprobe task. Upon completion of all three tasks, participant filled in the self-report version of the Liebowitz Social Anxiety Scale (LSAS-SR; Fresco et al., 2001; Liebowitz, 1987), the Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001) and the short version of the Empathy Quotient (EQ; Baron-Cohen & Wheelwright, 2004) in the respective order. As the questionnaire scores were not included into the main analyses, descriptive statistics of these measures can be found in Table 1 in Online Resource 2. The total duration of the study was approximately 90min.

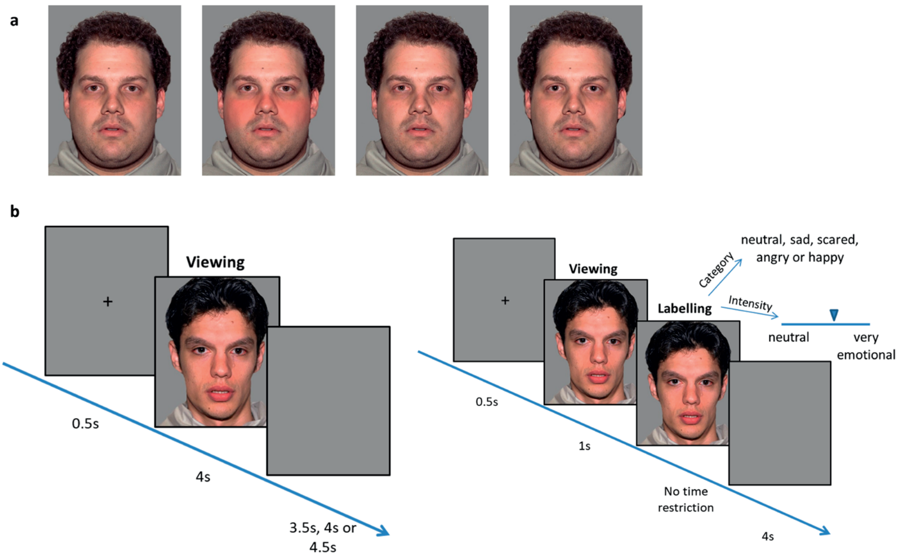

Figure 1. (a) Visualization of the subtle cue stimuli for one stimulus identity. The respective neutral facial expression from the NimStim set of Facial Expressions (first; Tottenham et al., 2009) was manipulated by adding a blush (second), tears (third) or dilated pupils (last). (b) Trial structure of the Passive Viewing task (left) and the Emotion Labelling task (right).

Measurements

Pupil size. Eyetracking data was recorded using a Tobii X2-60 eyetracker (sampling rate 60 Hz) to which event markers were sent via the presentation software. Filtering of the data as well as artifact identification and rejection were undertaken in the PhysioData Toolbox (Sjak-Shie, 2019) according to the guidelines described in Kret and Sjak-Shie (2019).

EMG. Facial muscle activity related to the observation of emotional expression was measured over Corrugator supercilii and Zygomaticus major regions (in the following referred to as "corrugator" and "zygomaticus"). In total, five 4mm reusable AG/AgCl surface electrodes were attached on the participant's face: two over each region of interest in the left side of the face and one ground electrode on the centre of the forehead, just below the hairline, according to the guidelines by Fridlund and Cacioppo (1986). Data was recorded with the Dual Wireless EMG BioNomadix System (Biopac, 2000 Hz sampling rate). The initial preprocessing of the raw EMG data was performed in the PhysioData Toolbox (Sjak-Shie, 2019). Before rectification of the signal, a 28Hz high-pass FIR, a 200Hz low-pass FIR and a 50Hz (Notch) filter were applied to the EMG data.

Skin conductance. The electrodes measuring changes in SCL were attached to the index finger and the ring finger of the participant's non-dominant hand. Data was recorded with the EDA 100C Biopac Systems module from (2000 Hz sampling rate, Gain: 5µV, 10Hz low-pass filter) and event triggers were sent from the presentation software via parallel port. Within the PhysioData Toolbox (Sjak-Shie, 2019), the recorded data was filtered with a 2Hz low-pass filter (Chênes et al., 2013).

Skin temperature. A fast response thermistor (TSD202A, Biopac) was placed below the participants' right cheekbone to record changes in cheek temperature. Data was acquired with the SKT100C Biopac Systems module (2000 Hz sampling rate,: Gain 2°F/V, 10Hz low-pass filter). Similar to the other measures, the PhysioData Toolbox (Sjak-Shie, 2019) was used for further filtering (1Hz low-pass; Chênes et al., 2013).

Data analysis

In order to shed light on different aspects of the processing of emotional expressions, we defined three different analyses aiming at the investigation of (1) subjective interpretation, (2) physiological signal changes and (3) the linkage between the two levels, see Fig. 2 for a visualization and further explanation. Since the study was not specifically designed to perform the third analysis, it should be considered as a pilot test and further information can only be found in Online Resource 4. Prior to the analysis of the data, we looked for irregularities in each dependent variable. Importantly, for the physiological measures, we integrated information from a repeated visual inspection with statistical and literature-based thresholds. An overview of the outlier criteria can be found in the Online Resource 1. In addition, missing trials in the EMG, SKT and SCL recordings were replaced with missing values (subject 8: 3 trials and subject 21: 2 trials). The data for all physiological channels within the windows of interest was downsampled by exporting average values within five 100ms time bins prior to stimulus onset for the baseline window and 75 100ms time bins after stimulus onset for the response window. Lastly, a baseline correction was performed by subtracting the baseline from all data points of the corresponding response window for each trial. While the entire response window (4 seconds stimulus presentation and 3.5 seconds blank screen) was used in the analysis of the relatively slowly changing SCL and SKT signals (M. E. Dawson et al., 2016; Shearn et al., 1990), EMG activity was only examined during stimulus presentation (Kret, Roelofs, et al., 2013; Kret, Stekelenburg, et al., 2013). In order to avoid distortions by the initial light reflex following stimulus onset (M. M. Bradley et al., 2008), the analysis on pupil size changes was restricted to the last two seconds of stimulus presentation.

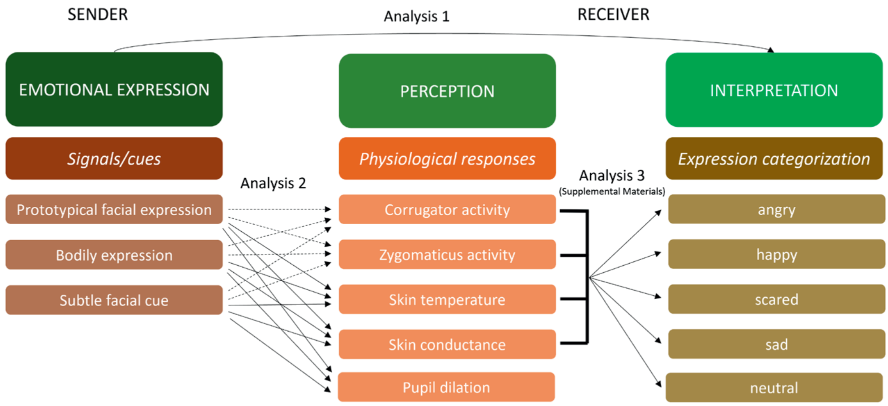

Figure 2. Visualization of the three analysis approaches. In Analysis 1, the subjective interpretation (emotion recognition and intensity judgments) of the different emotional expressions was examined. In Analysis 2, the effect of perceiving different emotional expressions belonging to the same modality on the shape of five different physiological signals was explored. In Analysis 3, trial-wise summary measures of expression-specific signal changes in all physiological channels were taken to fit a model on self-reported emotion labels and the generalizability of these observed patterns was evaluated using different data sets (test sample, inaccurate trials and subtle emotional cues; see Online Resource 4 for a more detailed description).

Analysis 1 (Behavioural analysis)

In the behavioural analysis, we investigated whether the specific content of the emotional expressions (categories: happy, angry, sad or fearful versus neutral) as well as the modality with which it was displayed (face versus body) had an influence on recognition performance as well as on the perceived intensity in the ELT. Thus, in the first step, we looked at differences in the accuracy of recognizing specific emotional expressions from different expression modalities. Investigating the data on a trial level, we fitted a binomial generalized linear mixed-effects model on accuracy (0 or 1) with emotion category, expression modality, and an interaction between the two of them as predictors. In order to account for individual differences in overall emotion recognition abilities, we included a random intercept for the subject variable.[3]

3 An addition of random slopes for emotion category and/or expression modality resulted in convergence issues. To keep the behavioral models consistent, we refrained from defining random slopes in any of the models.

In order to examine whether the perceived intensity of an emotional expression systematically varied depending on expressed emotion and/or the expression modality, we fitted a linear mixed-effects model on the intensity ratings of each participant with regard to the facial and bodily expressions. As in the analysis above, emotion category, expression modality and an interaction between the two of them were defined as fixed effects and we added a random intercept for each subject.

Finally, we examined the ratings of subtle facial cues. Given that their nature was largely different from the other stimuli (i.e. artificially created and exclusively added to neutral facial expressions), we kept the analysis for this modality separate. Further, we focused on their perceived intensity since there is no past evidence to indicate that a specific emotion is associated with these cues, hence, they cannot be accurately labelled (see Table 2 in Online Resource 2 for an overview of the provided emotion labels). Thus, we used cue type (tear, blush, dilated pupils versus no cue/neutral) as the sole predictor in the LMM on the intensity scores and added a random intercept for the subject variable.

All three models were fitted using the lme4 package (v1.1-23; Bates et al., 2015) in R 3.6.3 (R Core Team, 2020). After fitting a model, post-hoc pairwise comparisons between factor levels and their interactions were calculated by contrasting estimated mariginal means with the emmeans package (v1.4.8; Lenth, 2023). Reporting the test results of all pairwise comparisons would exceed the scope of this paper which is why they are listed in the Tables 3-8 in Online Resource 2. Online Resource 2 also contains the description and results of analyses in which we explored the effect of demographic and personality variables on emotion recognition performance and perceived intensity of emotional expressions.

Analysis 2 (Physiological analysis)

In the analysis of physiological data, we were specifically interested in identifying expression-specific changes in the shape of each physiological signal related to passive viewing of emotional expressions. Thus, we aimed to describe the entire time course in the response window of interest which differed in duration depending on the signals' temporal dynamics (see Data preprocessing). For modeling changes in pupil size, SKT and SCL, we extended the approach from studies looking at factors affecting pupil dilatation (Quesque et al., 2019; Wehebrink et al., 2018) and employed higher-order polynomials in Linear Mixed Models (LMMs). Given the fast changes in EMG activity related to affective states (Van Boxtel, 2010) as well as variations in response shapes (Cacioppo et al., 1988), we did not expect higher-order polynomials to reliable capture signal changes in the two EMG channels within the 4 seconds response window. In previous research on perception of static emotional expressions, EMG data was mostly analyzed over time periods of 1.5 – 2.5 seconds (Bornemann et al., 2012; Hermans et al., 2009; Rymarczyk et al., 2011, 2016; Sato et al., 2008) and, even if longer time windows were looked at, the EMG signal was averaged over time (Kret, Stekelenburg, et al., 2013; Vrana & Gross, 2004). To keep the temporal resolution similar across measures and still allow for a fine-grained description of the EMG time courses, we therefore chose to identify time bins in which the stimulus content affected the signal rather than describing the signal as a whole, similar to the approach of Achaibou and colleagues (Achaibou et al., 2008). The two analysis approaches will be outlined in more detail below.

Pupillometry, skin conductance & skin temperature. The time courses of the pupil size data, SCL data and the SKT data were modeled using growth curve analysis (Mirman, 2014) with the nlme package (Pinheiro et al., 2022) in R statistic (R Core Team, 2020). Three separate analyses were done for the three emotional expression modalities (prototypical facial expressions, bodily expressions and subtle facial cues). LMMs were fitted as follows: In order to capture the shape of the signal, first- and second-order orthogonal polynomials were used to model changes in pupil size, and first-, second- and third-order polynomials were chosen for the SCL and SKT models based on visual inspection of the overall shape of the time courses per subject. Within each expression's modality, emotion category (subtle: cue type) of the stimulus was included as categorical predictor (prototypical facial/bodily: angry, happy, sad, fearful and neutral; subtle: blush, dilated pupils, tears and neutral). Since these predictors of interest were assumed to influence the shape of the signal, interactions with the polynomials were added as fixed-effects to the models. Given the observed individual differences in the overall shape of the time series, a random intercept and random slopes of the polynomials were defined on a subject level. In order to account for autocorrelation between subsequent data points, an autoregressive structure with trials nested in subject as grouping factor was included. The Nelder-Mead technique was chosen as optimization method. Given the complex model structure, we increased the maximum number of iterations as well as the maximum number of iterations for the optimization step inside optimization (msMaxIter) up to 5000, and the number of iterations for the EM algorithm (niterEM) as well as the maximum number of evaluations up to 1000. Since the model residuals were not normally distributed, we additionally applied clustered bootstrapping to estimate the confidence intervals of the coefficients. Thus, in addition to the parametric approach of determining statistical significance of fixed effects with conditional *F*-Tests and marginal significance of fixed-effect coefficients conditional *t*-tests, their respective non-parametric confidence intervals were calculated. Given the large number of statistical parameters, only the results of the *F*-tests and the interpretation of the analysis will be reported in the text whereas the *t*-statistics and the nonparametric confidence intervals can be found in Tables 1-6 in Online Resource 3. Based on previous findings (M. M. Bradley et al., 2008, 2017; Kosonogov et al., 2017; Lang et al., 1993), we additionally explored the possibility whether overall emotional intensity, instead of specific emotion expression categories, could explain a large amount of variation in the physiological signal changes (see Online Resource 3, Tables 10-12 and Fig. 2). Given that our stimuli were not controlled for global and local brightness and contrast, pupil size changes related to emotional content might have been altered in our analyses. For conciseness, these results are only reported in Online Resource 3 (Tables 7-9 and Fig. 1).

Facial EMG. Since there was no empirical evidence to expect any exact shape of the two EMG signals throughout our stimulus presentation window (4 seconds), our analysis aimed to determine the parts of the signal in which a specific emotional expression differed significantly from the respective neutral expression. Here, we extended on an approach by Achaibou and colleagues (2008) who tested for significant differences in EMG activity during stimulus presentation by calculating t-tests between activations related to angry versus happy facial expressions in 100ms time bins. In contrast to their analysis, however, we (1) ran multilevel models instead of t-tests (including random variation and using the nlme package (Pinheiro et al., 2020), in consistence with the other here reported analyses), (2) compared each emotion category (happy, angry, fearful and sad) against neutral as a control condition and (3) used a split-half approach (i.e. first tested for effects in half of the sample [training set] and then validated the significant results in the other half [test set]). The two sets were matched by gender but, apart from that, randomly generated. This third adjustment was taken to allow for hypothesisfree exploration in one half of the data and confirmatory tests in the other half (Wagenmakers et al., 2012). As for the pupil size data, the SCL data and the SKT data, separate analyses were performed for the different expression modalities. Further, data from the corrugator region and the zygomaticus region were analysed separately and, similarly to Achaibou et al. (2008), only two conditions were contrasted in one test (i.e. one emotion category against neutral). Thus, for each of the 40 100ms time bins and for each presented emotional expression, we fitted separate LMMs on the mean EMG activity (filtered + rectified, see preprocessing) of the corrugator and the zygomaticus with emotion category as fixed effect and ID as random effect on the test sample. If one emotion category was significantly different from neutral in a time bin ($p < .05$), the same model was tested using the data from the test sample. Only if the difference between the signal related to the emotional versus the neutral expression was significant in both the training and the test sample, the EMG signal was regarded to be affected by the presentation of the respective emotional expression within this time bin.

Results

Behavioural results (Analysis 1)

Descriptive statistics of the behavioural responses can be found in Table 1 in Online Resource 2. Contrasting expectations based on the stimulus validation studies (de Gelder & Van den Stock, 2011; Tottenham et al., 2009), recognition rates were lower for bodily expressions ($M = 0.776$, $SD = 0.098$) compared to the prototypical facial expressions ($M = 0.885$, $SD = 0.081$). The recognition rates of the same bodily expressions in the original validation study are higher but our results are in line with the means that were obtained in Kret, Stekelenburg et al. (2013).

Prototypical facial and bodily expressions of emotion. The model on accuracy in emotion recognition yielded significant main effects of emotion category, $\chi2(4) = 185.788$, $p < .001$, and modality (body versus face), $\chi2(1) = 39.921$, $p < .001$. Importantly, the significant interaction between emotion category and expression modality, $\chi2(4) = 203.438$, $p < .001$, sheds more light on the interplay between the two variables affecting accuracy in emotion recognition (see Fig. 3a below and Table 3 in Online Resource 2). Overall, while emotions were better recognized compared to a neutral expression when expressed by the face, the opposite was observed for the body. Specifically, within the bodily expressions, the neutral expression was significantly better recognized than all emotional bodily expressions, except for fear. Fearful body expressions were better recognized than angry and happy bodily expressions. Finally, both angry and sad bodily expressions were more likely to be labeled correctly than their happy counterparts. In contrast, when emotions were presented on the face, happy facial expressions were best recognized, followed by angry facial expressions, and thirdly faces expressing fear, which received higher accuracy rates than sad facial expressions (all *p*-values ≤ 0.029). Lastly, neutral facial expressions were least well recognized. When comparing between modalities, there was no difference in the Odds for labeling sad facial and bodily expressions accurately. However, while angry, happy and fearful expressions were more likely to be accurately recognized when they were displayed on the face, neutral expressions were more easily recognized from the body (see Table 4 in Online Resource 2).

Both emotion category and modality were significant predictors in the model on perceived emotional intensity, category: $F(4, 5521) = 420.987$, $p < 0.001$; modality: $F(1, 5521) = 3.865$, $p = 0.049$. The significant interaction between the two predictor variables highlighted their interdependency, $F(4, 5521) = 37.339$, $p < 0.001$ (see Fig. 3b and Table 5 in Online Resource 2). Within the facial expression modality, intensity ratings were lower for sad expressions compared to the three other emotions and both happy and fearful expressions received lower intensity scores than angry expressions but did not significantly differ from each other. In contrast, happy expressions received the second lowest intensity scores for the bodily expressions and were rated significantly lower in intensity than angry, sad and fearful expressions while these three did not significantly differ from each other. When comparing the two expression modalities, angry, happy, neutral and fearful expressions were all perceived as more intense when they were displayed on the face whereas there was no difference for sad expressions (see Table 6 in Online Resource 2).

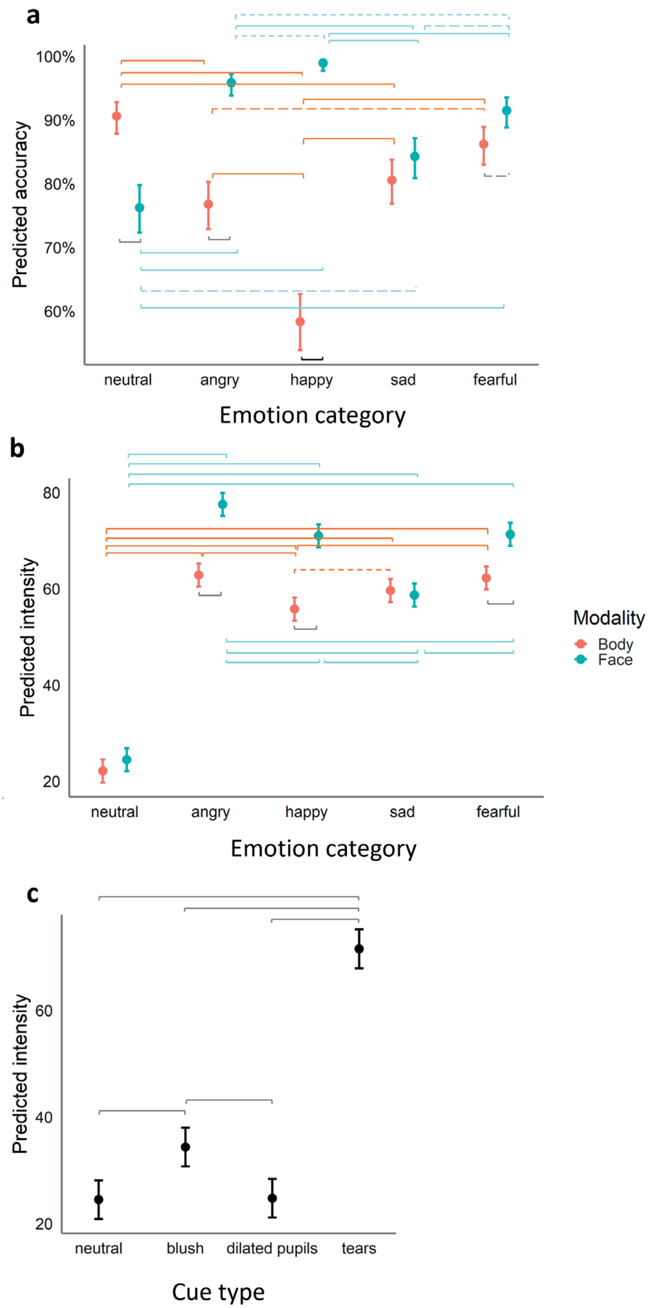

Figure 3. (a) Predicted accuracies of labeling stimuli belonging to the four emotion categories (angry, happy, sad, fearful) and neutral within the body (red) and face (blue) modality and (b) their respective predicted intensity ratings. Predicted intensity ratings for the subtle facial expressions by cue type are illustrated in (c). Whiskers represent confidence intervals. Significant differences between factor levels are

indicated by adding a bracket (red = between categories within bodily expressions, blue = between categories within facial expressions, grey = within category across modalities OR between subtle cue types). Straight line = $p < .001$, dashed line = $p < .01$, dotted line = $p < .05$

Subtle facial cues. A separate model on the perceived intensity of the subtle facial cues revealed that the presence of a cue was a significant predictor of the intensity rating, $F(3, 2097) = 669.31$, $p < 0.001$. Crucially, faces with dilated pupils were rated equally intense as the same expressions with average pupil sizes (neutral). In contrast, stimuli with a blush received higher ratings than both neutral faces and faces with dilated pupils. Faces with tears were rated as significantly more intense than faces with the two other cue types and compared to neutral (see Fig. 3c and Tables 7 and 8 in Online Resource 2).

3

Physiological results (Analysis 2)

Skin conductance

Prototypical facial expressions. In the LMM, the linear polynomial was a significant predictor of the changes in SCL, F_{linear} (1,181345) = 9.457, $p = 0.002$. Further, all interactions between emotion category and the three polynomials were significant, $F_{linear*category}$ (4,181345) = 5.596, $p < 0.001$; $F_{quadratic*category}$(4,181345) = 12.274, $p < 0.001$; $F_{cubic*category}$(4,181345) = 15.145, $p < 0.001$, indicating that the shape of the signal differed for emotional as compared to neutral expressions. Looking at the t-statistics (Table 1 in Online Resource 3) as well as the predicted value graphs (Fig. 4a) for distinct emotion categories, the presentation of angry, happy and sad facial expressions were more strongly associated with an initial peak at around 2s and a decline over time which was strongest for happy expressions. A cubic component in the signal was observed following fearful faces, which however was not as strong as the other categories and without the pronounced peak at the beginning. Notably, only the interaction between angry facial expressions and the cubic trend did not include 0 in the bootstrap confidence intervals for the model coefficients, indicating that exclusively this effect was robust.

Bodily expressions. As for the model on facial expressions, the linear polynomial significantly predicted SCL measurements, F_{linear} (1,181420) = 9.981, $p = 0.002$. In addition, the linear and cubic polynomials were involved in significant interaction terms with emotion category ,$F_{linear*category}$ (4, 181420) = 22.935, $p < .001$; $F_{cubic*category}$ (4, 181420) = 5.541, $p < .001$, suggesting that the expression of emotion via the body also had an effect on the shape of SCL measurements. In this modality, however, only happy and, to lesser degree, fearful expressions were related with an increase in SCL magnitude whereas angry expressions rather yielded a stronger decline compared to neutral expressions (see Fig. 4B). While, in general, SCLs also decreased over time for sad bodily expressions, this decrease followed a cubic shape compared to neutral expressions. The bootstrap analysis could not confirm the robustness of directionalities of effects in this model (see Table 2 in Online Resource 3 for all statistics).

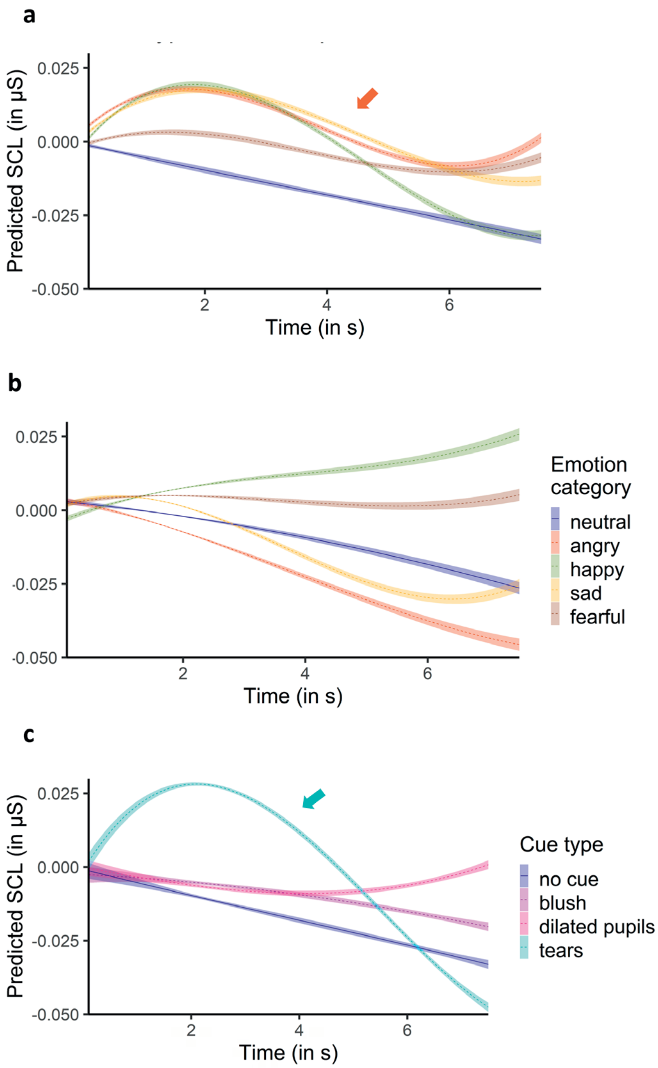

Figure 4. Predicted time course of the baseline-corrected skin conductance level signal (SCL) related to passive viewing of (a) prototypical facial expressions and (b) bodily expressions by emotion category as well as (c) subtle facial cues by cue type. The shaded areas indicate standard errors of the predicted means. Coloured arrows indicate robust results in the clustered bootstrap analysis.

Subtle facial cues. In the last SCL model, the linear polynomial was again identified as significant predictor, F_{linear} (1,140024) = 8.855, p = .003, as were the interactions between all three polynomials and emotion category, $F_{linear*category}$ (3, 140024) = 16.339, p < 0.001; $F_{quadratic*category}$(3, 140024) = 45.746, p < 0.001; $F_{cubic*category}$ (3, 140024) = 11.745, p < 0.001. Thus, the presence of facial signs of emotional involvement, without the context of prototypical emotion displays, also affected SCL properties: based on the statistics (Table 3 in Online Resource 3) and predicted time courses (Fig. 4c) for the three cue types versus neutral (no cue), the SCL signal decreased to a lesser degree for faces with an added blush and faces with dilated pupils, with even a slight late increase for the latter. Moreover, when observing faces with added tears, SCLs of participants increased steeply, with a peak around 2.5s and a fast decline. Importantly, the coefficient for the interaction between the quadratic trend and tears cue category was the only coefficient which was consistently below 0 in the bootstrap samples, pointing out the stability of the observed peak in SCL for tears.

3

Skin temperature

Prototypical facial expressions. While only the linear polynomial and the cubic polynomial were significant predictors of the SKT signal in the response window, F_{linear} (1,182620) = 5.622, p = .018; F_{cubic} (1, 182620) = 4.909, p = 0.027, all interactions between the three polynomials and emotion category became significant model terms, $F_{linear*category}$ (4, 182620) = 8.518, p < .001; $F_{quadratic*category}$(4, 182620) = 6.948, p < .001; $F_{cubic*category}$ (4, 182620) = 4.757, p = .001. Emotional versus neutral facial expressions therefore also seemed to affect changes in SKT differently. Looking at the model statistics (Table 4 in Online Resource 3) and predicted value plots (Fig. 5a), there was a stronger increase in SKT following happy and fearful expressions and a diminished late increase following angry expressions compared to neutral ones. In addition, after an initial increase, cheek temperature already declined after approximately 6s for sad and fearful expressions while this was not the case for the other facial expression categories. Importantly, no coefficient for any predictor was consistently larger or smaller than 0 in the bootstrap analysis.

Bodily expressions. In the model describing SKT changes associated with viewing bodily expressions of emotions, the linear polynomial as well as the three interactions between each polynomial and emotion category were significant, F_{linear} (1, 182845) = 4.220, p = .040; $F_{linear*category}$ (4, 182845) = 9.937, p < .001; $F_{quadratic*category}$(4, 182845) = 20.160, p < .001; $F_{cubic*category}$ (4, 182845) = 6.151, p < .001. Examining the effect of emotion in a body posture on the shape of the signal more closely, SKT rose for all emotions compared to neutral (Fig. 5b). However, while this increase was roughly linear for angry expressions, both happy and fearful expressions were related to a more cubic-like signal shape with stronger increases at the very beginning and end of the response window. On top of that, SKT first decreased after viewing sad expressions and only started to increase after approx. 2.5s. The coefficient describing this initial dip was also the only coefficient for which the confidence interval of the bootstrap analysis did not include zero, indicating its stability (see Table 15 in Online Resource 3 for an overview).

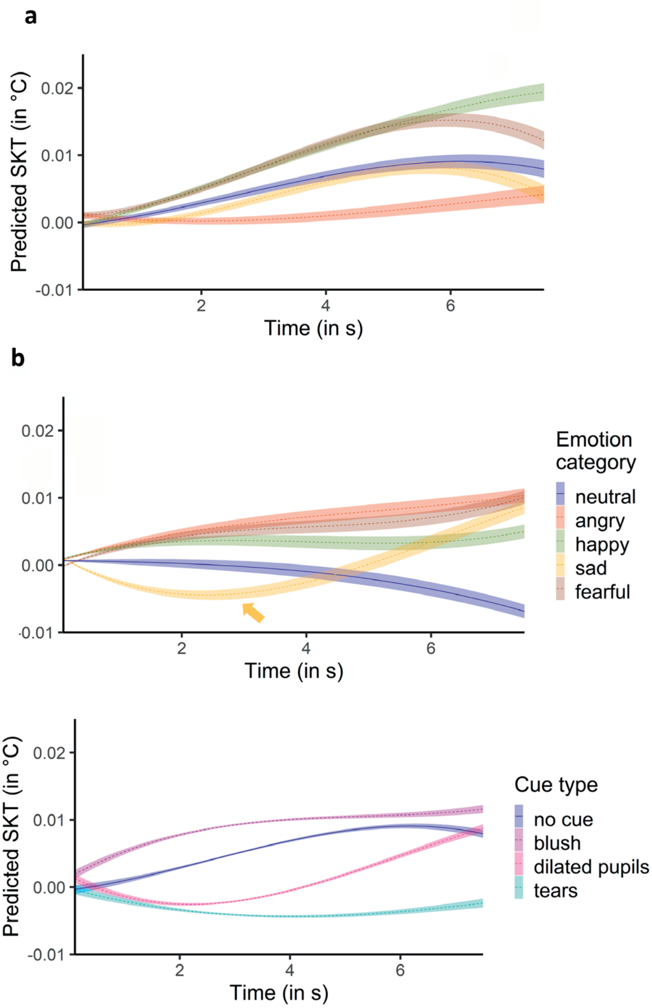

Figure 5. Predicted time course of the baseline-corrected skin temperature signal (SKT) related to passive viewing of (a) prototypical facial expressions and (b) bodily expressions by emotion category as well as (c) subtle facial cues by cue type. The shaded areas indicate standard errors of the predicted means. Coloured arrows indicate robust results in the clustered bootstrap analysis.

Subtle facial cues. Both linear and cubic polynomials significantly predicted changes in SKT in the subtle facial cue model, F_{linear} (1, 141599) = 7.225, p = .007; F_{cubic} (1, 141599) = 5.227, p = .022. Additionally, all interactions between the emotion category and the three polynomials were significant , $F_{linear*category}$ (3, 141599) = 5.543, p = 0.001; $F_{quadratic*category}$(3, 141599) = 24.200, p < .001; $F_{cubic*category}$ (3, 141599) = 5.095, p = 0.002. Thus, adding subtle emotional cues to a neutral picture might already make a difference in the characteristics of SKT changes in the observer. Consulting the model statistics (Table 6 in Online Resource 3) and the predicted value graph (Fig. 5c), both faces with added tears and faces with added dilated pupils were associated with an initial dip. While this dip turned into an increase after approximately 2s for the first (reaching a similar temperature level as the faces without cue), it did not for the latter. Faces with a blush yielded a strong increase in cheek temperature which attenuated over time. The subsequent bootstrap analysis did not support the directionality of any of the effects.

3

Facial EMG

Corrugator supercilii. The split-half tests on differences in facial muscle activity between emotional and neutral expressions within distinct time bins yielded emotion- as well as time-specific findings. When viewing happy compared to neutral facial expressions, activity over the corrugator supercilii region was significantly reduced in both our training and test sample 500ms, 600ms, 1600ms and 3800ms after stimulus onset (all ps < 0.05). Further, while 200ms and 600ms after stimulus onset, angry facial expressions yielded lower EMG activity compared to neutral expressions, the same observation was made for fearful facial expressions 3600ms after stimulus onset. Lastly, we did not find a replicable effect of sad facial expressions on the EMG signal (see Fig. 6a below and Table 13 in Online Resource 3). The analyses on the other expression modalities revealed that neither any of the emotional bodily expression nor any of the emotional facial cues had a consistent effect on the Corrugator signal in the training and the test sample.

Zygomaticus major. EMG activity over the zygomaticus major region was consistently elevated for happy versus neutral facial expressions starting 700ms after stimulus onset and almost throughout the entire stimulus presentation (700ms – 2600ms, 2800 - 2900ms, 3200 - 3900ms; all ps < .05). Moreover, seeing a fearful facial expressions was related to an enhanced EMG signal 1800-2200ms after stimulus onset in both training and test sample. Activations during the presentation of both angry and sad facial expressions did not differ significantly from neutral expressions (see Fig. 6b and Table 14 in Online Resource 3). On top of that, activity over the Zygomaticus major region was not observed to be altered if any of the emotional bodily expressions or facial cues compared to their neutral counterparts were shown.

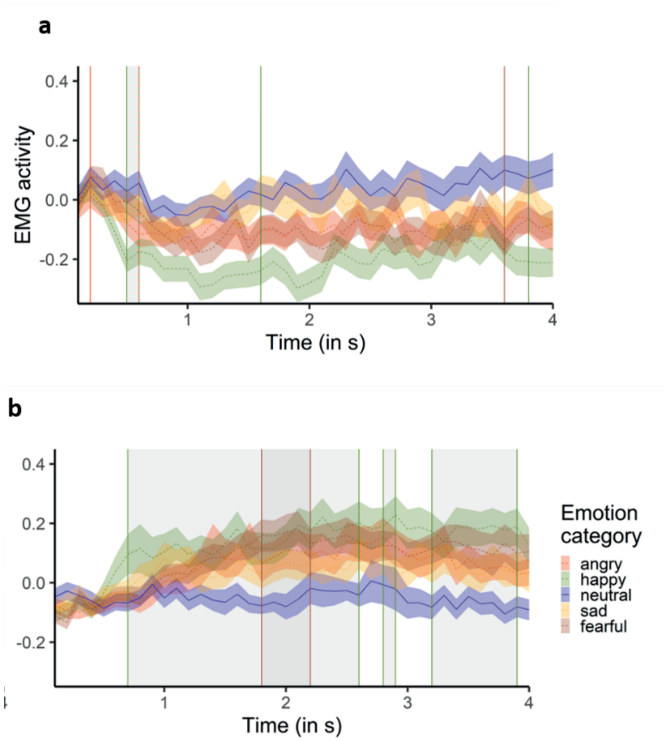

Figure 6. Time course of the filtered, baseline-corrected and z-scored facial electromyography (EMG) signal over (a) the corrugator supercilii region and (b) the zygomaticus major region related to passive viewing of prototypical facial expressions by emotion category. The coloured shaded areas around the values indicate standard errors of the predicted means. Signals were plotted and analyzed in time bins of 100ms each. Coloured vertical lines (and grey-shaded background areas between them) highlight time bins in which the EMG signal when viewing an emotional expression is significantly different from neutral in both samples (training and test), with the colour indicating the corresponding emotion category.

Discussion

The aim of our study was to explore how expressions of emotion resonate in an observer's body and mind. There are three main findings: First, the results show that, while participants distinguished between different emotional expressions in self-reports, physiological changes were not strictly corresponding to distinct emotion categories. Even though there was no 1-1 relationship between perception and physiological response, some robust physiological responses could be linked to the perception of certain emotional expressions, i.e. a peak in SCL for angry facial expressions and a decrease in SKT for sad bodily expression. Second, specific facial muscle (de-)activations were reproducibly observed following facial but not bodily expressions of emotion. Third, faces with tears were not only perceived as emotionally intense, but also elicited a robust peak in observers' skin conductance levels. In the remainder of the discussion, we will discuss these findings in more details.

Overall, participants were well able to recognize all emotional expressions. However, they did show variation across expression modalities as well as emotion categories: Apart from displays of sadness, emotional facial expressions were better recognized than emotional bodily expression, with happy faces being most easily identified (Kret, Stekelenburg, et al., 2013; Martinez et al., 2016). One driving factor of this finding might be the intensity of the expression which has been suggested to play a crucial role in recognizing both emotions from the body (Aviezer et al., 2012) and the face (Hess et al., 1997). Happy facial expressions, together with fearful facial expressions, received the second-highest intensity ratings in our study which might have facilitated their recognition. While bodily expressions were shown to be especially informative for the recognition of high-intensity emotions (Aviezer et al., 2012), the presented emotional body stimuli in our study were predominantly rated as less intense than their facial counterparts. Only facial and bodily expressions, which were also similarly well recognized, did not differ in their intensity ratings. Our study thus confirms that intensity might be a relevant factor in the recognition of emotional expression. Given the overall high accuracy rates, our results further support that humans are highly capable of identifying and discriminating a variety of emotional expressions (A. S. Cowen & Keltner, 2019; Witkower & Tracy, 2019).

The clear distinction between emotions in self-reports was not reflected in participants' physiology. Nevertheless, a few consistent relationships between discrete emotion categories and physiological markers were observed. Specifically, in the SCL signal, a cubic trend with an early peak appeared when participants observed angry facial expressions. This result is in line with previous studies, showing that observing negative facial expressions (Banks et al., 2012), and anger in particular (Kreibig, 2010), tend to increase SCL (but see Vrana & Gross, 2004 for different results). As signals of direct threat, angry faces take a special role in emotion perception. Compared to other emotional expressions, their detection and processing occurs in a privileged, speedy and automatic manner (Feldmann-Wüstefeld et al., 2011), a phenomenon called the "anger-superiority effect" (Hansen & Hansen, 1988). Perceiving threat immediately sets the body in a fight-or-flight mode (Cannon, 1914), which is typically characterized by autonomic arousal and, among others, with an increased SCL (Darrow, 1936). This may explain the observed increase in SCL in our study, with the early peak highlighting the fast processing of facial displays of anger as a potential threat.

The current study also yielded some novel findings related to the processing of sad expressions. Sadness is characterized by a low-arousal physiological state (Huron, 2018) and a conservation-withdrawal tendency which, however, is not consistently reflected across physiological channels (Kreibig et al., 2007). When observing sad body expressions, the participants in the current study showed an initial drop in their cheek temperature (see Salazar-López et al., 2015 for similar findings on negative images with low arousal). As previous research has shown that watching sad body movements can induce sadness in observers (Shafir et al., 2013), the cheek temperature drop in our study might be the result of induced sadness. Compared to other facial regions, cheek temperature variations have however not been extensively studied in the context of emotional responses yet (Clay-Warner & Robinson, 2015; Ioannou et al., 2014). Further research should therefore substantiate this suggestion. Apart from these two observations, we did not find evidence for a robust linkage between the perception of basic emotion displays and distinct ANS responses. Our findings, thus, challenge the idea that their own signals from the ANS could serve observers as a reliable indication of the observed individual's state.

One characteristic of facial emotional expressions is that they tend to be mimicked (e.g., Bornemann et al., 2012; Rymarczyk et al., 2011; Varcin et al., 2019), which is believed to help their recognition (Niedenthal, 2007; Palagi et al., 2020). Our examination of facial muscle responses revealed that happy facial expressions were not only best recognized in the current study, but also elicited the most prominent and prolonged changes: an increase in zygomaticus activity and a decrease in corrugator activity, replicating previous findings(e.g., Rymarczyk et al., 2011; Vrana & Gross, 2004). The question arises why smiles, compared to the other expressions, yielded such strong effects. In daily life, humans are constantly exposed to smiling faces, making it the most frequently observed expression (Somerville & Whalen, 2006). These smiles can have different meanings and may signal reward, dominance or affiliation (Martin et al., 2017). In line with their assumed function to create and maintain social bonds (Keltner, 1995), past research has shown that smiles are frequently reciprocated in social interactions (Hess & Bourgeois, 2010). The relevance of smiles in interpersonal bonding might therefore be one explanation for the pronounced mimicry of smiles in our study. In addition, smiles have also been found to be mimicked without the observer being directly addressed (e.g., see Mojzisch et al., 2006) These congruent facial responses have further been linked to specific neural activations in areas associated with embodiment and self-other distinction (Schilbach et al., 2008, see also Schilbach, 2015a). According to the Simulation of Smiles model (SIMS; Niedenthal et al., 2010), congruent facial responses to smiles in a non-communicative context can also be based on knowledge–based simulations of the other's emotional state instead of 'real' emotional contagion. Given that only expressions from the same modality, i.e. the face, and with high social signaling value, i.e. a smile, elicited facial muscle responses in the current study, embodied simulation might be a plausible explanation for our EMG findings. Without necessarily evoking the experience of happiness, the simulation of smiles could potentially even have facilitated emotion recognition (however, see Holland et al., 2020).

Crying is claimed to be a uniquely human behavior and linked to a complex pattern in ANS responses, with sympathetic activation being most consistently found (Bylsma et al., 2019). Another key finding of the current study is that faces with tears were perceived as emotionally intense and increased sympathetic arousal in the participants when observing these stimuli. More specifically, the addition of tears to a neutral expression resulted in a steady peak in the observers' SCL. Other research has demonstrated that tears increase the perceived sadness in others and, thereby also the wish to help them (Küster, 2018). Perceiving tears thus seems to elicit approach behaviour and, induces sympathetic arousal. Despite the scarce research on physiological responses to the observation of crying individuals, our findings substantiate the suggested function of tears as an effective call for social support (Balsters et al., 2013; Gračanin et al., 2018) by highlighting their strong resonance in the observer.

The above-described results include all robust findings of our study. Apart from these results, various other, non-robust emotion-specific effects on the physiological measures require further examination. At this moment, these effects should be considered specific to our sample and not be generalized. Most remarkably, these physiological effects show a great divergence across the different expression modalities and emotion categories in our stimulus materials. The most prominent example of this is the emotion of anger which, compared to the respective neutral expressions, was responded to with an increase in SCL if shown in the face and a decrease in SCL if expressed by the body. In contrast, the exact opposite pattern became apparent in the SKT responses to angry faces (SKT decrease) and angry bodies (SKT increase). This lack of coherence between physiological channels is in line with our first key finding and complements evidence against an 'all-or-none' activation of the sympathetic nervous system and for a more differentiated view of ANS targets (Ax, 1953; Kreibig, 2010). Moreover, while bodily expressions of emotion were described to be automatically integrated in the processing of facial emotional expressions and facilitate their recognition (de Gelder, 2006; Kret, Stekelenburg, et al., 2013; Poyo Solanas et al., 2018), isolated expressions from the two modalities might not automatically resonate similarly in an observer's body.

From a functional standpoint, the limited extent of a consistent autonomic tuning to prototypical emotional expressions does make sense: Instead of requiring affect sharing for informative or affiliative purposes, our passive viewing task provided subjects with a stream of static and posed displays of emotion without a relevant social context (Fridlund, 1991; Hess & Fischer, 2013). The use of static images posed a limitation concerning ecological validity as compared to real dynamic expressions (Krumhuber et al., 2013). Further, our participants were automatically put in the role of a passive observer, knowing that a displayed individual was not receiving any information about their own expressions. Importantly, the opportunity to interact with a social stimulus has been described to be highly influential in social attention (Laidlaw et al., 2011). Similarly, knowing that the counterpart has access to one's own expressions can alter observational tendencies, enhance social signalling and promote prosocial choices(Cañigueral & Hamilton, 2019; Frith, 2009; Gobel et al., 2015). The degree of interactivity with a stimulus may thus determine the quality and strength of responses on multiple levels, including physiological signals (Schilbach et al., 2013). Based on experimental evidence looking at different aspects of social cognition and behaviour, Schilbach and colleagues (2013) called for a turn to a 'second-person neuroscience': Social phenomena should be investigated in real social settings with two (or more) actively-involved individuals, allowing to examine dynamics between, rather than only within, individuals. In the past years, this approach yielded promising insights in the behavioural and neural mechanisms underlying social interactions (Redcay & Schilbach, 2019). Recent findings successfully expanded an interactive viewpoint to the physiological level: Cooperation as a facet of prosocial behaviour was found to be positively associated with two interactants' synchronisation in SCLs (Behrens et al., 2020). Synchrony in SCLs, as well as in heart rate, was further shown to be predictive of interpersonal attraction (Prochazkova et al., 2021). Consequently, while facial mimicry of discrete emotions might inform the automatic categorization of emotional expressions in passive observers, the ANS might only be strongly activated by social signals in real social settings, with the dynamics between interactants reflecting their (emotional) alignment.

In the future, researchers should try to keep experimental paradigms as close to real life situations as possible. In cases in which passive observation of stimuli is required, it can already be beneficial to use dynamic and naturalistic, non-posed expressions (Kret et al., 2020). Compared to static and posed emotional expressions, these types of stimuli elicit stronger facial mimicry (Rymarczyk et al., 2011; Sato et al., 2008). In attempts to link physiological changes with subjective experiences of others' emotions, it would, additionally, be interesting to include measures of interoceptive abilities. As understanding one's own body has already successfully been linked to understanding one's own emotions (Critchley & Garfinkel, 2017; Kanbara & Fukunaga, 2016), accurate interoceptive inferences might also be important prerequisites to connect to others' emotions (Arnold et al., 2019).

To sum up, we confirmed existing evidence that the interpretation of emotional expressions depends on both the modality of the expression as well as the affective content. However, even if only information from the face or the body was available, emotion signals were still accurately perceived. Given that these situations become more frequent due to digitalization or safety measures during the COVID-19 pandemic, it is reassuring to know that emotion recognition as an essential process is not severely affected. Using static and posed expressions, we found limited evidence for a physiological signature of discrete emotions in the observer. The robust effects which we found might occur as a result of social cues eliciting strong motivational tendencies (e.g. SCL peaks in response to tears or angry faces) or embodied simulation of frequently observed expressions (e.g. EMG responses to happy faces). Based on recent perspectives on social cognition, an actual alignment in emotional states, which goes beyond emotion recognition, might however only happen in a 'real' social context. As a consequence, in order to describe a link between the sharing of emotions on different levels of observation (experiential and physiological), future studies should involve interactive paradigms and examine the role of variables indexing an individual's access to internal signals. A mechanistic understanding could eventually inform the development of interventions which target the identification of other's emotions and, thus, facilitate building social connections.

Chapter 4

Facial Mimicry and Metacognitive Judgments in Emotion Recognition are Distinctly Modulated by Social Anxiety and Autistic Traits

Abstract

Facial mimicry as well as the accurate assessment of one's performance when judging others' emotional expressions have been suggested to inform successful emotion recognition. Differences in the integration of these two information sources might explain alterations in the perception of others' emotions in individuals with Social Anxiety Disorder and individuals on the autism spectrum. Using a non-clinical sample (N=57), we examined the role of social anxiety and autistic traits in the link between facial mimicry, or confidence in one's performance, and emotion recognition. While participants were presented with videos of spontaneous emotional facial expressions, we measured their facial muscle activity, asked them to label the expressions and indicate their confidence in accurately labelling the expressions. Our results showed that confidence in emotion recognition was lower with higher social anxiety traits even though actual recognition was not related to social anxiety traits. Higher autistic traits, in contrast, were associated with worse recognition, and a weakened link between facial mimicry and performance. Consequently, high social anxiety traits might not affect emotion recognition itself, but the top-down evaluation of own abilities in emotion recognition contexts. High autistic traits, in contrast, may be related to lower integration of sensorimotor simulations, which promote emotion recognition.

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Data availability statement:
The datasets and materials generated and/or analysed during the current study are available on Dataverse NL:
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Supplementary material:

The expression "her face says it all" exemplifies the fundamental contribution of nonverbal signals and cues in the communication of inner states (Frith, 2009; Tracy et al., 2015). According to social-functional approaches, emotional expressions are crucial in guiding social interactions by informing about others' states, evoking coordinated emotional responses, and incentivizing social behaviour (Keltner & Kring, 1998; van Kleef & Côté, 2021). The accurate identification of an observed emotional expression is a key component in the interpretation of an expresser's emotional state, yet links between emotion recognition and other processes underlying emotion perception are still not well described. Facial mimicry, that is the mirroring of an observed expression, is one process that has been suggested to promote the recognition of others' emotions (Buck, 1980; Künecke et al., 2014) (see Facial mimicry paragraph for further details). In contrast to this bottom-up information channel, the top-down assessment of one's recognition performance, a metacognitive process, might also provide relevant feedback about emotion processing (Kelly & Metcalfe, 2011)(see Metacognition paragraph for further details). Importantly, alterations in the processing of others' emotions, as well as in mimicry and metacognition (Davies et al., 2016; Rouault et al., 2018) have been reported for various mental health and neurodevelopmental conditions, such as Social Anxiety Disorder (SAD) and Autism Spectrum Disorder (ASD). Research in both clinical populations has further revealed a link between alterations in processing other's emotional expressions and social interaction difficulties (Gilboa-Schechtman & Shachar-Lavie, 2013; D. A. Trevisan & Birmingham, 2016). The current study examines the putative associations between facial mimicry and confidence in emotion recognition abilities (i.e., a metacognitive judgment) with actual emotion recognition performance, as well as their potential alterations associated with social anxiety and autistic traits.

Mimicry and Emotion Recognition

When observing an individual expressing an affective state via the face, people tend to automatically mirror the observed facial expression—a phenomenon called facial mimicry (Dimberg, 1982). Distinct changes in activity over two muscle regions, the Zygomaticus Major and the Corrugator Supercilii (for simplicity referred to as "zygomaticus" and "corrugator" hereinafter) have been consistently reported in response to videos of emotional displays: Strongest evidence has been found for an increase in zygomaticus activity when happy facial expressions were viewed, together with a decrease in corrugator activity (Dijk, Fischer, et al., 2018;

Hess & Blairy, 2001; Künecke et al., 2014; Olszanowski et al., 2020; Rymarczyk et al., 2011, 2016; Sato et al., 2008). Enhanced corrugator activity, in contrast, has been linked to the perception of anger displays (Dijk, Fischer, et al., 2018; Hess & Blairy, 2001; Künecke et al., 2014; Olszanowski et al., 2020; Peter-Ruf et al., 2017; Sato et al., 2008) and, less pronounced, for sadness displays (Hess & Blairy, 2001; Künecke et al., 2014; Olszanowski et al., 2020).

Importantly, instead of being only an epiphenomenon, facial mimicry has been proposed to aid emotion recognition (Drimalla et al., 2019; Künecke et al., 2014; Sato et al., 2013). In line with seminal theories on emotion (Damasio, 1996; James, 1884), peripheral signals, such as facial expressions, can not only inform the producer about the physiological effects of emotions via interoceptive pathways (Critchley & Garfinkel, 2017). "Facial feedback" (Buck, 1980) might also act as an information source when another individual's expression is automatically mirrored, serving as a sensorimotor simulation of another person's emotional state (Wood et al., 2016). This view was supported by studies that showed a decline in emotion recognition performance if facial mimicry was voluntarily (Stel & van Knippenberg, 2008) or artificially (Neal & Chartrand, 2011) blocked. Yet, recent meta-analyses suggest that the effects of facial feedback on affective judgments, including emotion recognition, are not consistent (Coles et al., 2019; Holland et al., 2020). Moreover, facial mimicry does not seem to be a requirement for successful emotion recognition: A study in patients with Möbius syndrome has shown that, despite facial paralysis, these patients could still accurately recognize emotional expressions(Bogart & Matsumoto, 2010).

Metacognition and Emotion Recognition

Metacognition describes the monitoring of one's own cognitive processes and has been claimed to be an immanent feature of human social interactions (Frith, 2012). Nevertheless, it is scarcely researched in the domain of emotion recognition. According to the few available studies on emotion recognition in healthy adults, a reliable metacognitive resolution (i.e., a clear subjective discrimination between correct and incorrect recognition), together with a general overconfidence has been found (Bègue et al., 2019; Dentakos et al., 2019). Furthermore, only direct trial-by-trial ratings, which can be used to estimate 'relative meta-accuracy', and not global beliefs about one's abilities, were found to be predictive of performance in emotion recognition tasks (Kelly & Metcalfe, 2011).Thus, while global metacognitive beliefs seem to be biased, confidence in one's emotion recognition skills (i.e., a metacognitive judgment) can act as a reliable feedback mechanism in an emotion recognition context.

Emotion Recognition Alterations in SAD and ASD

While emotion recognition difficulties have sporadically been reported in SAD (Montagne et al., 2006), most research did not find lower accuracies (Bui et al., 2017) or even found a higher sensitivity, reflected by an emotion detection at lower expression intensities, to emotional expressions (Arrais et al., 2010; Joormann & Gotlib, 2006). Heightened attention to social cues also stands at the basis of established theoretical models of SAD (Clark & Wells, 1995; Rapee & Heimberg, 1997) and has predominantly received support in form of a "negativity bias" (Amin et al., 1998; Hirsch & Clark, 2004; Machado-de-Sousa et al., 2010). In other words, negative expressions automatically attract more attention and are avoided at the same time, they are integrated more strongly in judging the self in social interactions, they are remembered better, and even ambiguous expressions are more likely to be judged negatively. Correspondingly, not clinically diagnosed individuals with high social anxiety trait levels have shown an emotion recognition advantage (Hunter et al., 2009), and specifically better recognition of negative expressions (Gutiérrez-García & Calvo, 2017b; Richards et al., 2002). For individuals on the autism spectrum, in contrast, difficulties in visual emotion recognition paradigms in which emotional facial or bodily expressions had to be matched to samples or labelled have mainly been described for all basic emotions, and, particularly, for fear (Frank et al., 2018; Sucksmith et al., 2013; Uljarevic & Hamilton, 2013) (however, see (Mazzoni et al., 2022)). Thus, quite specific particularities in facial emotion recognition have been associated with SAD and ASD. Factors that could be linked to, and potentially even contribute to, the occurrence of those particularities are, however, not well described yet.

In past research, individual differences in autistic traits and social anxiety traits have also been related to the usage of different strategies to recognize emotional expressions. When labelling full-body emotional expressions, high compared to low socially anxious individuals have been shown to attend to faces less, and more to expressive hands, thus using different visual cues (Kret et al., 2017). In a study comparing recognition of sadness in static facial expressions versus point light displays, only individuals with low autistic traits, compared to individuals with high autistic traits, showed a recognition advantage for sad faces. Fear, in contrast, could be better recognized in point-light-displays by individuals with low autistic traits, and in faces by individuals with high autistic traits (Actis-Grosso et al., 2015). These findings suggest that, depending on clinical trait levels, different features might be used to identify others' emotional states. Recently, it has even been suggested more broadly that emotions reach awareness via different pathways in individuals on the autism spectrum compared to neurotypical individuals (Arnaud, 2020). Differences in processing facial emotional expressions, despite unimpaired emotion matching performance, have already been reported in autistic children on a neural level (Corbett et al., 2009). In our study with healthy participants, we aimed to explore whether the link between emotion recognition and two processes that have been suggested to promote emotion recognition, namely facial mimicry and metacognitive judgments, differs depending on social anxiety and autistic traits.

Altered Mimicry in Emotion Recognition in SAD and ASD

Studies investigating the effects of social anxiety (disorder) on facial mimicry have reported inconsistent results: while some studies found intact mimicry in non-clinical but high socially anxious individuals (Dijk, van Emmerik, et al., 2018; Peter-Ruf et al., 2017), others demonstrated enhanced mimicry of negative expressions and diminished mimicry of positive ones (Dimberg, 1997; Vrana & Gross, 2004) or stronger differential muscle activity between happy and angry expressions, for both the zygomaticus and the corrugator (Dimberg & Thunberg, 2007). The literature on ASD gives a clearer picture: Reduced automatic mimicry in individuals on the autism spectrum has been reported in many studies (Davies et al., 2016; D. A. Trevisan et al., 2018). Importantly, this reduction could not be explained by a generally lower facial expressiveness or an inability to mimic expressions, but by a mismatch between observed and produced facial muscle activity patterns (McIntosh et al., 2006; Rozga et al., 2013; Weiss et al., 2019). Only few studies have described differences in facial mimicry alterations between different emotion categories, and findings are inconsistent. Namely, mimicry of angry, but not happy, facial expressions was reduced with higher autistic trait levels in females in one study (Hermans et al., 2009), while reduced mimicry of happy, but not sad, expressions has been related to higher autistic traits in another study (Tan et al., 2020). Whether observed reductions in facial mimicry in high autistic trait levels are also linked to differences in emotion recognition performance has, however, not directly been investigated yet.

Altered Metacognition in Emotion Recognition in SAD and ASD

Reduced metacognitive abilities have been proposed as a shared characteristic in different psychiatric disorders (Nordahl et al., 2019; Rouault et al., 2018). Theoretical accounts on the development and maintenance of SAD have highlighted the importance of a negatively biased view on one's own performance in a social context (Clark & Wells, 1995; Rapee & Heimberg, 1997), together with an excessive monitoring of the self (Hartman, 1983). This global negative judgment of one's own abilities might have evolved via repeated underestimation of (social) abilities (Müller-Pinzler et al., 2019). However, metacognitive abilities in emotion recognition have yet not been directly tested in individuals with SAD. In contrast, the few studies on metacognitive judgments of social cognition in individuals on the autism spectrum have suggested a complex pattern of alteration. Some studies reported no differences between neurotypical individuals and individuals on the autism spectrum in calibrating confidence judgments to emotion recognition performance, that is, higher confidence rating for more accurate or faster recognition (Sawyer et al., 2014; S. Wang & Adolphs, 2017). A more recent study, however, found evidence for both an over- and underconfidence in contrast to actual performance in social cognitive tasks, including emotion recognition, in individuals on the autism spectrum compared to neurotypical individuals (DeBrabander et al., 2020). Both expressing low confidence in accurate trials as well as high confidence in incorrect trials should be reflected in a reduced metacognitive sensitivity, which Fleming and Lau (Fleming & Lau, 2014) defined as "the extent to which confidence discriminates between correct and incorrect trials" (p. 2). Given the limited knowledge about metacognition in the domain of emotion recognition and its relation to SAD and ASD, the current study aimed to explore two assumptions: (1) whether the negatively biased assessment of one's performance in social situations in people with high social anxiety trait levels also translates to emotion recognition, and (2) whether the decreased metacognitive sensitivity related to higher autistic traits in the social-cognitive domain also specifically holds for emotion recognition performance.

Objectives of the Current Study

In the current study, we examined whether social anxiety and autistic traits modulate the links between facial mimicry and emotion recognition as well as between confidence judgments in own emotion recognition skills and emotion recognition. To investigate this, our participants first passively viewed naturalistic video clips of different facial expressions of emotion while we measured their facial muscle activity. In a subsequent task, participants indicated how strongly they associated the expressions with distinct emotion categories and were asked how confident they were in their judgments. Despite sharing social interaction difficulties in the global disorder definitions, previous research on emotion recognition, facial mimicry, and metacognitive judgments showed specific alterations associated with SAD and ASD. Therefore, we also expected to find distinct modulations for the two trait dimensions.

More specifically, confirming the suggested heightened sensitivity to social cues, higher levels of social anxiety were expected to be related to a recognition advantage of facial expressions, resulting in higher accuracy rates. According to the negativity bias findings, this advantage should be specifically pronounced for negative expressions (i.e., anger, fear, and sadness). As individuals with SAD have been found to report a generalized underconfidence in their social skills, we expected that, despite an improved emotion recognition performance, elevated social anxiety traits would be related to reduced overall confidence in the performance. Moreover, based on observations that confidence judgments were predictive of emotion recognition accuracy in healthy subjects, we would like to explore whether the scaling of confidence judgments to actual emotion recognition performance is altered depending on social anxiety traits. In line with a proposed facilitating role of facial mimicry in emotion recognition, stronger facial mimicry might be assumed with higher social anxiety traits. Empirical evidence for both relationships, social anxiety (disorder) and facial mimicry as well as facial mimicry and emotion recognition, is, however, inconclusive. Therefore, we aimed to directly test whether the role of facial mimicry in emotion recognition is altered depending on an individual's social anxiety traits.

Regarding autistic traits, we expected to observe an overall worse recognition of naturalistic dynamic facial expressions in association with higher levels of autistic traits, which should be most pronounced for fearful faces. Higher autistic trait levels were further expected to be associated with less facial mimicry, and this reduction was expected to be strongest for negative expressions. Furthermore, as automatic facial mimicry has been suggested to be impaired in ASD, the information about facial muscle activity might also be less well integrated in emotion recognition. Accordingly, we explored whether a positive relationship between facial mimicry and emotion recognition would be less pronounced in individuals with higher autistic trait levels. Lastly, extending on the few findings in clinical samples, we expected lower metacognitive sensitivity in relation to higher autistic traits. Hence, confidence judgments should be less predictive of actual emotion recognition accuracy in individuals with higher autistic trait levels. Given the little and inconclusive evidence on metacognition in emotion recognition in healthy and clinical populations, our analyses regarding this research question were explorative.

Methods

Participants

Fifty-seven healthy participants were recruited from the Leiden University student population (50 female and seven male). Their ages ranged from 18 to 30 years old (M = 22.75, SD = 3.27) and they all reported normal or corrected-to-normal vision. None of the participants reported current or past psychological or neurological disorders. Participation in the study was voluntary and written consent was obtained prior to the experiment. Participants received either two university credits or a monetary reward of six euros as reimbursement. The study has been executed in accordance with the Declaration of Helsinki and approved by the local ethics committee of the Faculty of Social and Behavioral Sciences at Leiden University (# 2020-02-10-M.E. Kret-V1-2117).

In the scope of a Master thesis project, an a priori power analysis was run for this study, treating clinical traits as a categorical variable (low vs. high trait levels). Based on a similar previous study that found significant group effects with medium effect sizes (Zwick & Wolkenstein, 2017), we estimated our ideal sample size with the Power Analysis for General ANOVA application (PANGEA) (Westfall, 2015). With 30 participants per group, hence 60 participants in total, a group effect of d = .50 should be found with a power of .901. Because of the COVID-19 regulations in the Netherlands, we had to stop data collection prematurely and ended up with 57 participants in total (56 participants: power of .879). For the analyses in this manuscript, we treated the clinical trait dimensions as continuous variables, thereby increasing the validity of the approach as well as statistical power (Altman & Royston, 2006).

Stimuli

Following the call for more naturalistic stimuli in research on emotion perception, we chose the FEEDTUM database (Wallhoff et al., 2006) as a source for our stimuli. This database encompasses videotaped spontaneous (i.e., non-instructed) reactions to video clips inducing the six different basic emotions and neutral control expressions. All depicted individuals provided informed consent for the usage of the videos for research purposes, including distribution and publication of the material, in the original study. Permission to use the material under CC-by and to publish example images in scientific journals, such as in Fig.1, was granted to the first author of this study by the creators of the database. Based on the choice of stimuli in a previous study investigating facial mimicry and emotion recognition in depression (Zwick & Wolkenstein, 2017)', we included facial expressions of anger, fear, happiness, sadness, surprise, and neutral. Disgust was not included, which is a basic emotion that (next to surprise) is typically less investigated in studies on emotion recognition alterations in SAD and ASD (Bui et al., 2017; Uljarevic & Hamilton, 2013). For each facial expression, video clips of ten individuals (five females and five males) were selected based on the following decision pipeline: First, videos were judged on their quality, and blurry or shaky videos were excluded. Second, individuals wearing glasses or individuals with hair in front of their eyes were excluded as these features made their facial expressions more difficult to recognize. Lastly, all remaining video clips were evaluated by the automated facial expression recognition software FaceReader 7.1 (Noldus, 2014) to ensure that the emotion label of the stimulus provided by the database could also be detected in the video. After this selection procedure, the video clips were cut to a uniform length of 2 seconds (500ms neutral expression followed by 1500ms of each category's expression). Lastly, the video clips were standardized by removing the original backgrounds using Adobe After Effects (Christiansen, 2018), and by replacing them with a uniform gray colored background (RGB color code: 145, 145, 145). This led to a total of 60 two-second videos with a grey background showing ten individuals (five males and five females) per facial expression.

Procedure

Participants were brought to a quiet room, in which they were given written and verbal instructions about the experimental procedure. After filling in the informed consent form, electrodes were attached to the participants' faces for the facial electromyography recordings (see Measurements section). During the tasks, participants were seated in 50cm distance of a Philips screen with a resolution of 1920 x 1080 pixels (23.6"), on which the stimuli (720 x 480 pixels, average visual angle: 22.12° horizontal and 14.85° vertical) were presented using E-Prime 3.0 software (Psychology Software Tools, 2016). The grey background colour of all screens was set to the background colour of the stimuli (RGB color code: 145, 145, 145). The same 60 emotional facial expression videos were presented in a random order in two consecutive tasks, a passive viewing task during which the participants' facial muscle activity was recorded, and a facial emotion recognition task. The rationale behind the two separate tasks was to avoid that participants would be biased in their perception and their facial mimicry responses in the passive viewing task by being aware of the possible emotion category labels (i.e., top-down modulation). In the passive viewing task, participants were instructed to only look at the stimuli without performing any action. Each trial started with the presentation of a black fixation cross against a grey background for one second, and was followed by one of the 60 video stimuli for two seconds. The end of a trial was marked by a grey inter-trial interval (ITI) screen, which appeared with a jittered duration of either 5750, 6000, or 6250ms. To account for the possibility of missing observations due to noisy data, participants viewed each of the 60 videos twice, in two separate blocks, resulting in 120 trials in total. Between the blocks, participant could take a self-paced break. The passive viewing task lasted around 20 minutes in total. After the passive viewing task, the electrodes were detached from the participants' faces and the experiment continued with the facial emotion recognition task. In this second task, the participants viewed all 60 video stimuli once again (thus three times in total) but were now instructed to answer questions about them. Similar to the passive viewing task, each trial started with the fixation cross screen for one second and one of the 60 video stimuli (2s) was presented afterwards. Once the video disappeared, participants were asked to judge the displayed expression. More specifically, on the first question screen, they were asked to rate the expression according to its representativeness of the six expression categories that could be displayed: anger, fear, happiness, neutral, sadness, and surprise ('To what degree does the expression relate to the emotions below?'). Each expression category was accompanied by horizontal sliders ranging from 'not at all' to 'very much' and participants had to move the slider to indicate their judgment. The values of the sliders ranged from 0 to 100 in steps of 10 (0, 10, 20, etc.), which were not visible to the participants. The next screen contained three questions: (1) 'How intense was the expression displayed in the video?' to measure perceived emotional intensity; (2) 'Are you confident about your decision?' to measure confidence in own performance; and (3) 'Did you find the trial simple?' to measure simplicity (Zwick & Wolkenstein, 2017). Again, all questions were accompanied by a slider ranging from 'not at all' to 'very much' with underlying values ranging from 0 to 100 in steps of 10. Thus, higher scores indicated higher ratings on perceived intensity, confidence, and simplicity, respectively. After the second question screen, a grey inter-trial interval (ITI) screen appeared for three seconds. In total, the participants completed 60 trials, rating all stimuli from the first task, plus three additional practice trials showing a different individual to familiarize them with the task. After 30 trials, participants could take a self-paced break and the entire facial emotion recognition task lasted approximately 25 to 30 minutes. A visualization of one facial emotion recognition trial can be found in Fig. 1.

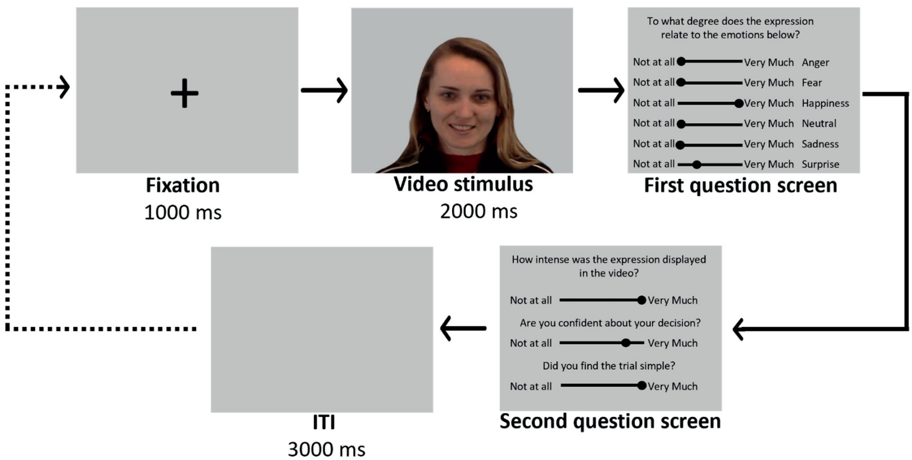


Figure 1. Illustration of a Facial Emotion Recognition task trial. Each trial started with a fixation screen and ended with an intertrial interval (ITI) screen. The dotted line indicates that this sequence was repeated until all 60 videos were presented once.

Importantly, only the ratings on the association of the displayed expression with the expression categories (first question screen) and the confidence ratings on the second screen were relevant to answer our hypotheses. As we did not formulate specific hypotheses about alterations in perceived emotional intensity ratings related to social anxiety or autistic traits, explorative analyses on this rating variable can be found in the Supplemental Materials. Furthermore, the simplicity ratings provided insights in how difficult emotion recognition with this novel stimulus set was perceived. Overall, happy expressions received the highest simplicity ratings (M = 69.39, SD = 27.15), followed by surprised expressions, (M = 62.51, SD = 25.35), fearful expressions (M = 50.93, SD = 26.19), angry expressions (M = 45.05, SD = 25.66), neutral expressions (M = 36.42, SD = 33.74), and sad expressions (M = 36.19, SD = 25.56). Some might consider differences in simplicity between emotion categories as potential confound in predicting emotion recognition accuracy (i.e., higher simplicity ratings might systematically be linked to more accurate choices). Yet, these differences have been proposed to arise due to factors that are inherently linked to the specific emotional expression, such as a higher familiarity with increased exposure in daily life (Calvo et al., 2014; Nummenmaa & Calvo, 2015). We aimed for higher ecological validity in examining facial emotion recognition by using spontaneous and non-acted expressions in the current study. Controlling for simplicity, in contrast, would detach our results from emotion recognition in everyday life, which is why we decided against it. Lastly, participants filled in the Liebowitz Social Anxiety Scale (LSAS) (Liebowitz, 1987) and the Autism Spectrum Quotient (AQ; see Measurements section) (Baron-Cohen et al., 2001). Upon completion of the experiment, participants were given a written and verbal debriefing about the goal of the study and were reimbursed. In total, the experiment lasted around 55 minutes, including instructions and the attachment of the facial electromyography electrodes.

Measurements

Facial Electromyography (fEMG)

Facial electromyography (fEMG) was measured on the left side of the face of all our participants, following the guidelines of Fridlund and Cacioppo (Fridlund & Cacioppo, 1986). To specify, two reusable 4 mm Ag/AgCl surface electrodes were placed over the Corrugator Supercilii region, which allowed us to measure mimicry responses to sad, fearful, and angry expressions (according to the EMFACS definition) as well as to happiness expressions (as shown in previous research). Other two electrodes were placed over the Zygomaticus Major region, which allowed us to measure mimicry responses to happy expressions. Additionally, a ground electrode was added on the top of the forehead. The signal was transmitted and amplified using a Biopac MP150 system combined with a BioNomadix 2 channel wireless EMG amplifier. Data recordings were made in AcqKnowledge 4.3 (Biopac Systems Inc, 2009) using a sampling rate of 1000 Hz. Event markers as defined in the E-Prime (Psychology Software Tools, 2016) tasks were sent via a parallel port and saved within an event marker channel. For data preprocessing, the EMG recordings were loaded into the PhysioData Toolbox (Sjak-Shie, 2019) in which they were rectified and filtered with a 28 Hz high cut-off filter, a 500 Hz low cut-off filter, and a 50 Hz notch filter. For each trial, separate epochs were defined for the fixation period (1s), the first 500ms of stimulus presentation in which a neutral expression was shown (later defined as *baseline*), the subsequent 1500ms in which the emotional expression was shown (later defined as *response*), and the first 1500ms of the blank screen after stimulus presentation. Within these epochs, the EMG signal was downsampled by calculating the average signal within consecutive 100ms time bins. The combined data from all subjects was then exported into MATLAB for further preprocessing. First, an automated artifact detection, which was inspired by Dignath et al. (Dignath et al., 2019), was conducted. More specifically, for each subject and each muscle region, we checked the distribution of the EMG signal for extreme values (+/- 3.5 SDs) in the time bins regarding the absolute value of each time bin and the relative differences between subsequent bins. This was performed in relation to (1) the entire time interval of interest per trial (5 baseline time bins and 15 response time bins) and (2) the distribution of baseline time bins in the same position across trials. If more than 50% of all time bins (20) or more than 50% of the baseline time bins (5) belonging to one trial had extreme values, this trial was entirely excluded from the analysis. Otherwise, the respective time bins were replaced with missing values. Across all subjects, 17 trials (0.002%) were excluded from the corrugator analysis and 150 trials (0.02%) from the zygomaticus analysis. After excluding the marked time bins, a baseline correction was performed by subtracting the mean EMG activity of all baseline time bins belonging to one trial from the respective response time bins. The baseline-corrected EMG data was then z-scored for each participant and each muscle region. Furthermore, the data was summarized on a trial level by averaging the last second of each trial's response window (last 10 time bins) for each participant and each muscle region as well as by averaging across the two presentations of each of the 60 stimuli to end up with the same amount of observations as for the rating data (trial-averaged data; used as predictor in generalized linear mixed models). Lastly, the data was also summarized on a participant level by creating the average of the same time window across trials for each participant, each muscle region and each emotion category (category-averaged, used as outcome variable in linear models).

Questionnaires

Social anxiety traits measure. We used the Liebowitz Social Anxiety Scale (LSAS) (Liebowitz, 1987) to measure self-reported social anxiety traits in our non-clinical sample. The LSAS is designed to assess fear and avoidance levels of individuals with social phobia in a range of social interaction and performance scenarios. The questionnaire contains 24 items in total. Respondents score the items for fear and avoidance separately on a 4-point Likert scale, fear: 0 (= None), 1 (= Mild), 2 (= Moderate), 3 (= Severe); avoidance: 0 (= Never), 1 (= Occasionally), 2 (= Often), 3 (= Usually). The scores are all added up to a total sum of all subscales, with higher scores indicating a higher severity of social anxiety symptoms. One participant had missing data for one questionnaire item and another participant had missing data for two questionnaire items, which were estimated using the mice-package(van Buuren & Groothuis-Oudshoorn, 2011) for multiple imputation. The LSAS showed an excellent internal consistency in our sample ($\alpha = 0.91$, 95% CI [0.88, 0.95]). LSAS scores ranged from 7 – 73 ($M = 38.53$, $SD = 17.53$), with 30 participants (52.63%) exceeding a score of 30. This score has been described as the best cut-off to discriminate between non-anxious individuals and individuals with SAD (Mennin et al., 2002; Rytwinski et al., 2009). Thus, a broad spectrum of social anxiety trait levels was covered in our sample, with half of the participants showing an indication of clinically relevant social anxiety. The average LSAS scores were considerably higher compared to the healthy validation sample of the LSAS self-report version ($M = 13.49$, $SD = 23.70$) (Fresco et al., 2001). With a skewness of 0.21 and a kurtosis of 2.08, the distribution of the LSAS scores showed to be slightly platykurtic, yet close to normal (see Fig.S1[A] in the Supplemental Material).

Autistic traits measure. The Autism-Spectrum Quotient (AQ) (Baron-Cohen et al., 2001) is a self-report questionnaire, which was created to measure traits associated with the autism spectrum. The AQ consists of 50 items in total and can be divided into five subscales (10 items each) assessing different domains: social skill, attention switching, attention to detail, communication, and imagination. Respondents indicate how strongly each item applies to them based on a 4-point Likert scale ranging from 1 (= definitely agree), 2 (= slightly agree), 3 (= slightly disagree), and 4 (definitely disagree), and some items are reversely scored to prevent response biases. All item scores are added up to a total sum score, with higher scores reflecting higher autistic trait levels. One participant did not complete the AQ and was therefore excluded from all analyses investigating effects of autistic traits. Furthermore, we had to estimate three single item scores using the mice-package (van Buuren & Groothuis-Oudshoorn, 2011) for multiple imputation as one participant did not respond to one item and another participant did not respond to two items. Internal consistency of the AQ in our sample was good, $\alpha = 0.83$, 95% CI [0.76, 0.89]. The range of AQ scores was between 2 – 39 (M = 16.38, SD = 7.34), which is highly similar to meta-analytic results on AQ scores in general population samples (M = 16.94, 95% CI [11.6, 20.0])(Ruzich et al., 2015). Only 3 participants (5.26%) had a higher AQ score than 32, which indicates autistic trait levels of clinical significance. The skewness and kurtosis of the AQ score distribution were 1.05 and 4.17 respectively, thus showing a positive skew (see Fig. S1B) in the Supplemental Material).

Data Analysis

Spearman's rank correlation revealed that autistic traits and social anxiety traits, reflected by the scores on the two questionnaires, were not significantly associated with each other, $r_s = 0.04$, $p = .784$. Our sample showed both variability within each trait dimension that was similar to studies with larger samples (see Questionnaire section) and independence between the trait dimensions, allowing for separate analyses for the two trait dimensions. Emotion recognition accuracy was calculated by determining the expression category with the highest slider score and comparing it to the predefined category of the stimulus for each trial (Zwick & Wolkenstein, 2017). If there was a match between the presented and the perceived expression category, a trial was scored as correct (1) whereas it was scored as incorrect (0) in case of a mismatch. Trials in which two expression categories received the same slider scores were discounted from the analysis. To check the robustness of this approach, we re-ran all analyses on accuracy with a relative accuracy score, which was calculated by subtracting the mean score of all other expression categories from score of the correct expression category (Keating et al., 2021). The results were overall highly similar and are reported in the Supplemental Materials. All analyses were performed in R 4.0.1 (R Core Team, 2020), using the lmerTest package (Kuznetsova et al., 2017) for fitting the (generalized) linear mixed models ([G]LMMs), the multcomp package (Hothorn et al., 2008) for general hypotheses testing, the sjPlot package (Lüdecke, 2021) for creating the tables and both the sjPlot package and ggplot2 (Wickham, 2016) for creating the plots.

Behavioural Analysis

Accuracy and confidence. In order to test whether social anxiety traits were associated with better emotion recognition performance for negative expressions and whether emotion recognition accuracy was generally reduced with higher autistic traits, we calculated two binomial GLMMs on accuracy with emotion category (anger, fear, happiness, sadness, surprise, and neutral), the respective trait dimension (autistic traits or social anxiety traits), and their interaction as fixed effects. Both participant ID and the identity of the stimulus were added as random effects (random intercept). Furthermore, we fitted two LMMs on emotion recognition confidence to test the association between confidence level and i) social anxiety traits, ii) autistic traits . The models had the same fixed and random effects structure as the accuracy models. Coefficients for the emotion categories (main effects and interactions) were calculated by contrasting each single category against the mean of all categories (sum coding) to determine significant deviations from mean accuracy (main effect) or the mean effect of a trait dimension (interaction). For the neutral category, coefficients were calculated and tested (z-tests) using general hypotheses testing. Lastly, we explored whether the relation between confidence and emotion recognition was altered depending on an individual's clinical trait levels as well as the presented expression. To do so, we added emotion recognition confidence and all 2-way interactions as well as the 3-way interactions with emotion category and the respective clinical trait dimension to the accuracy models. The resulting model fits were the following:

1. LSAS * EMOTION CATEGORY → EMOTION RECOGNITION ACCURACY
2. AQ * EMOTION CATEGORY → EMOTION RECOGNITION ACCURACY
3. LSAS * EMOTION CATEGORY → EMOTION RECOGNTION CONFIDENCE
4. AQ * EMOTION CATEGORY → EMOTION RECOGNTION CONFIDENCE
5. LSAS * EMOTION CATEGORY * CONFIDENCE → EMOTION RECOGNITION ACCURACY (exploratory)
6. AQ * EMOTION CATEGORY * CONFIDENCE → EMOTION RECOGNITION ACCURACY (exploratory)

4

Metacognitive sensitivity. To examine how well an individual's confidence ratings could distinguish between accurate and inaccurate trials in the emotion recognition task, we calculated the hit and false alarm rate pairs with increasing confidence levels (11, according to points on the Likert scale) for each subject and employed the area under the type 2 ROC curve (AUROC2) approach according to Fleming and Lau (Fleming & Lau, 2014). More specifically, each confidence level was taken as a criterion to distinguish between low and high confidence trials; starting with a criterion in which only zeroes were regarded as low confidence ratings and all higher values were regarded as high confidence ratings, up until a criterion in which all trials below the highest confidence rating (100) were regarded as low confidence trials and only the highest rating was regarded as high confidence. The resulting probabilities for hits, p(high confidence|correct), and false alarms, p(high confidence|incorrect), were plotted against each other for each confidence level. The resulting area under this ROC2 curve was taken as an index for the subject's metacognitive sensitivity, describing how well an individual's confidence ratings were scaled to actual emotion recognition accuracy. The link to each clinical trait was then tested with a correlational analysis.

Facial EMG Analysis

Facial muscle activity (mimicry). By measuring facial muscle activity over the Corrugator Supercilii and Zygomaticus major regions, we could assess mimicry responses to angry, happy, sad and fearful expressions, with neutral expressions acting as a reference category. In order to examine whether social anxiety traits are associated to an enhanced mimicry of specifically angry (negative) expressions, we fitted a linear model on the category-averaged corrugator activity (i.e., taking the mean corrugator activity of all trials belonging to the same emotion category) with emotion category, social anxiety traits and their interaction as fixed effects. We also aimed to explore zygomaticus activity for mimicry of happy expressions and, therefore, used the same independent variables to predict category-averaged zygomaticus activity (i.e., taking the mean zygomaticus activity of all trials belonging to the same emotion category). By replacing social anxiety traits with autistic traits in the other two linear models on category-averaged corrugator and zygomaticus activity, we then tested whether typical mimicry patterns are indeed reduced with higher autistic traits (i.e., less corrugator activity for negative expressions (specifically anger), less zygomaticus activity for happy expressions and less decrease in corrugator activity for happy expressions). Coefficients for the emotion categories (main effects and interactions) were calculated by contrasting the respective category against the neutral reference category. Since the residual plots of the two model fits on zygomaticus activity showed violation of the normality assumption as well as heterogeneous error estimates, we calculated non-parametric estimates of the predictor effects and confidence intervals, using 1000 bootstrap iterations, for these two models. As neither main effects of clinical traits nor interaction effects with emotion category were found, the results, including significant effects of emotion category on EMG activity, are reported in the Supplemental Materials (Tables S7 – S10).

Link between facial muscle activity (mimicry) and emotion recognition accuracy. As outlined in the introduction (see Mimicry and Emotion Recognition section), the association between facial muscle activity and emotions, including mimicry of expressions, is specific for each emotion category. Emotion recognition should only be informed by facial muscle activity that is in line with the assumed mimicry responses for the specific emotion (e.g., increase in zygomaticus activity and decrease in corrugator activity for happy expressions, and increase in corrugator for sad expressions). Therefore, we ran separate analyses for the emotion categories anger, happiness, sadness, and fear to investigate the relationship between intraindividual differences in facial muscle activity and emotion recognition accuracy in the context of varying clinical trait levels. Binomial GLMMs were fitted on emotion recognition accuracy with the trial-averaged EMG activity over the two muscle regions (corrugator and zygomaticus) as distinct predictors, as well as one of the clinical trait scores and both two-way interactions (8 models in total). Similar to the behavioural accuracy models, random intercepts were added for the subject as well as the stimulus identity. This resulted in the following models:

1. LSAS * CORRUGATOR → ANGER RECOGNITION ACCURACY
2. LSAS * CORRUGATOR + LSAS * ZYGOMATICUS → HAPPINESS RECOGNITION ACCURACY
3. LSAS * CORRUGATOR → SADNESS RECOGNITION ACCURACY
4. LSAS * CORRUGATOR → FEAR RECOGNITION ACCURACY
5. AQ * CORRUGATOR → ANGER RECOGNITION ACCURACY
6. AQ * CORRUGATOR + AQ * ZYGOMATICUS → HAPPINESS RECOGNITION ACCURACY
7. AQ * CORRUGATOR → SADNESS RECOGNITION ACCURACY
8. AQ * CORRUGATOR → FEAR RECOGNITION ACCURACY

Results

Behavioural Results

Accuracy in Emotion Recognition

Social anxiety traits. The first binomial GLMM on emotion recognition accuracy included emotion category, social anxiety traits, and their interaction as predictors. Results showed a significant main effect of emotion category, $\chi 2(5) = 702.880$, $p < .001$. Emotion recognition performance for happy, surprised, and neutral expressions was significantly better than average recognition performance, happy: $OR = 10.834$, $z = 10.797$, $p < .001$, surprise: $OR = 3.027$, $z = 7.654$, $p < .001$, neutral: $OR = 2.337$, $z = 6.420$, $p < .001$. In contrast, sad and fearful expressions were significantly worse recognized than average, $OR = 0.232$, $z = -14.336$, $p < .001$, and $OR = 0.066$, $z = -23.445$, $p < .001$ respectively. All the other effects or interactions were not significant. This suggests that recognition accuracy was predicted by the emotional content displayed in the video, independent of the level of social anxiety traits (see Fig. 2A). An overview of the model fit can be found in the Supplemental Material (see Table S1).

Autistic traits. The second binomial GLMM on emotion recognition accuracy included emotion category, autistic traits, and their interaction as predictors. Results showed a significant effect of emotion category, $\chi 2(5) = 666.374$, $p < .001$, a significant effect of autistic traits, $\chi 2(1) = 8.985$, $p = .003$, and a significant interaction between autistic traits and emotion category, $\chi 2(5) = 21.606$, $p = .001$. The overall negative association between autistic traits and emotion recognition accuracy, $OR = 0.763$, $z = -2.998$, $p = .003$, was most pronounced for fearful expressions, $OR = 0.637$, $z = -3.292$, $p = .001$. Recognition of sad expressions was less negatively affected by autistic traits compared to the overall performance, $OR = 1.322$, $z = 2.821$, $p = .005$, and similarly recognition of surprised expressions, $OR = 1.314$, $z = 2.067$, $p = .039$ (for all other effects and more detailed information, see Fig. 2B and Table S2 in the Supplemental Material). Thus, the expected overall negative association between autistic traits and emotion recognition performance seems specifically pronounced for fearful facial expressions.

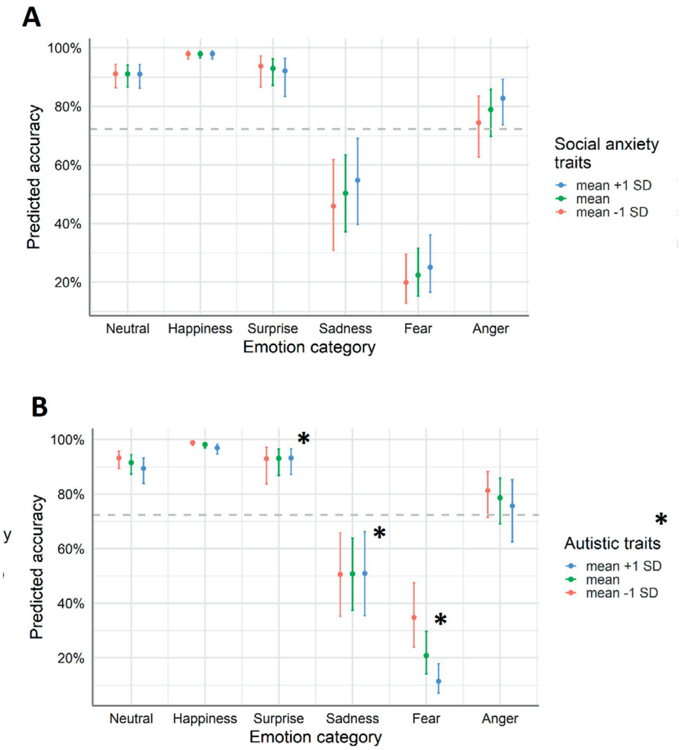


Figure 2. Predicted emotion recognition accuracies depending on (A) social anxiety trait levels and (B) autistic trait levels by emotion category (anger, fear, sadness, surprise happiness, neutral). In the model fits, accuracy was coded binomial (0-1 values). For illustrative purposes, predicted accuracies for mean values as well as mean values +/- 1 SD of the continuous variables social anxiety traits and autistic traits are depicted in percentages. Whiskers represent confidence intervals and significant effects are marked with an asterisk. The dashed horizontal line indicates mean predicted accuracy (across all categories and trait levels).

Confidence in Emotion Recognition

Social anxiety traits. In the first LMM on confidence in emotion recognition, with emotion category, social anxiety traits, and their interaction as predictors, significant effects of both emotion category, $F(5, 3344) = 118.666$, $p < .001$, and social anxiety, $F(1,3344) = 5.362$, $p = .024$, could be observed. Compared to the average confidence judgments across emotion categories, participants were significantly more confident in judging happy expressions, $\beta = 0.614$, $t(3344) = 19.695$, $p < .001$, neutral expressions, $\beta = 0.193$, $z = 6.186$, $p < .001$, and surprised expressions, $\beta = 0.084$, $t(3344) = 2.699$, $p = .007$. For the other emotional expressions, confidence was significantly reduced compared to the average, angry: $\beta = -0.247$, $t(3344) = -7.932$, $p < .001$, fearful: $\beta = -0.287$, $t(6761) = -9.209$, $< .001$, sad: $\beta = -0.356$, $t(3344) = -11.438$, $p < .001$. The association between social anxiety traits and confidence was negative, , $\beta = -0.132$, $t(3344) = -2.316$, $p = 0.024$, and did not vary by emotion category (i.e., no interaction). Thus, independent of the displayed expression, confidence judgments were significantly lower with higher social anxiety trait levels (for a detailed description of the model fit, see Fig. 3A and Table S3 in the Supplemental Material).

Autistic traits. In the LMM that included autistic traits instead of social anxiety traits to predict confidence in emotion recognition, the effect of emotion category was significant, $F(5, 3285) = 118.164$, $p < .001$, as was the interaction between emotion category and autistic traits, $F(5, 3285) = 9.531$, $p < .001$. While for neutral and happy facial expressions confidence was significantly reduced with higher autistic traits compared to the average effect of autistic traits on confidence ratings, β = -0.148, $z = -4.663$, $p <.001$, and β = -0.104, $t(3285) = -3.271$, $p = .001$ respectively, this effect was reversed for displays of fear and sadness. For those two categories, autistic traits were associated with higher confidence ratings compared to the average effect of autistic traits on confidence, fear: β = 0.102, $t(3285) = 3.229$, $p = .001$; sadness: β = 0.118, $t(3285) = 3.715$, $p < .001$ (see Fig. 3B and Table S4 in the Supplemental Material).

Link between Confidence and Emotion Recognition

Social anxiety and autistic traits. When exploring the link between confidence and accuracy in emotion recognition in relation to the clinical trait dimensions on a trial level and by emotion category, neither of the trait dimension had a substantial impact on this link (see Table S5 and S6 in the Supplemental Material for the entire model fits).

Metacognitive Sensitivity

According to Mahalanobis distance measures, two participants had to be excluded from the correlation analysis between social anxiety traits and AUROC2, and three participants had to be excluded from the correlation analysis between autistic traits and AUROC2. After excluding these bivariate outliers, all distributions did not majorly deviate from normality. The two correlational analyses between the clinical trait dimension and metacognitive sensitivity (AUROC2) revealed that autistic traits, but not social anxiety traits, were significantly related to metacognitive sensitivity (see Fig. 4). As expected, metacognitive sensitivity was reduced with higher autistic traits, $r = -.489$, $t(51) = -4.008$, $p < .001$ and $r_s = -.476$, $p < .001$. and no significant relation was found for social anxiety, $r = -.222$, $t(53) = -1.66$, $p = .103$ and $r_s = -.251$, $p = .064$.

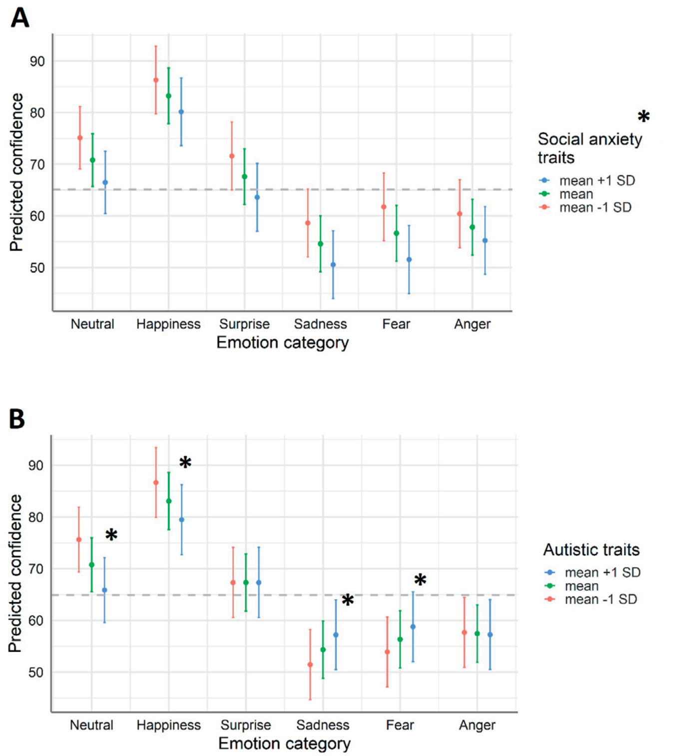


Figure 3. Predicted confidence in emotion recognition depending on (A) social anxiety trait levels and (B) autistic trait levels by emotion category (anger, fear, sadness, surprise happiness, neutral). For illustrative purposes, predicted accuracies for mean values as well as mean values +/- 1 SD of the continuous variables social anxiety traits and autistic traits are depicted. Whiskers represent confidence intervals and significant effects are marked with an asterisk. The dashed horizontal line indicates mean predicted confidence (across all categories and trait levels).

Facial Electromyography (fEMG) Results

Facial Mimicry in Emotion Recognition

Social anxiety traits. There was no significant interaction between corrugator activity and social anxiety traits in predicting emotion recognition accuracy of negative facial expressions, (i.e., anger, fear, and sadness, see Tables S11, S13 and S14 for the three model fits). The model on sad expressions did, however, reveal that accuracy was higher when the corrugator muscle was more strongly activated, $\chi^2(1) = 4.631$, $p = 0.031$, $OR = 1.585$. Furthermore, both zygomaticus activity as well as its interaction with social anxiety traits were significant predictors in the model on happy expressions, $\chi^2(1) = 4.331$, $p = .037$, $OR = 6.240$, and $\chi^2(1) = -2.017$, $p = .044$, $OR = 0.213$ respectively (Table S12 in the Supplemental Material). Hence,

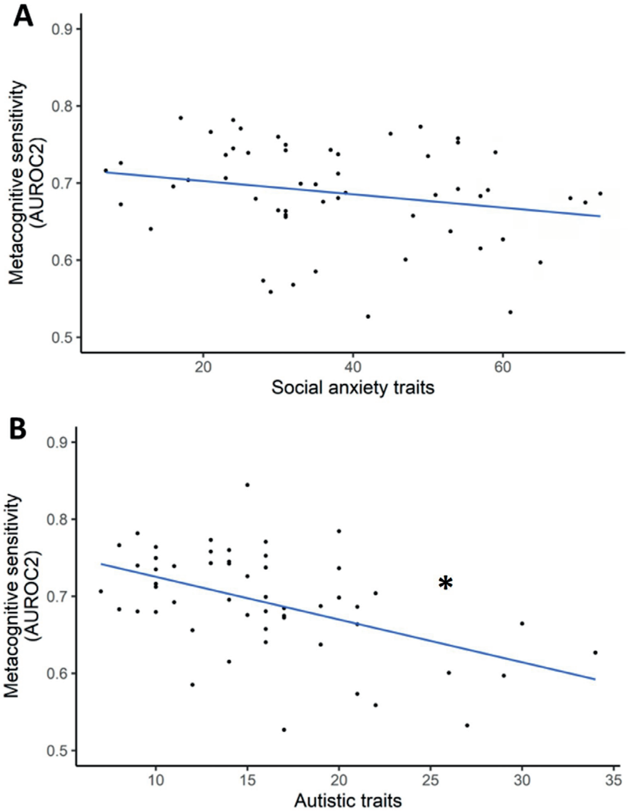


Figure 4. Relationship between (A) social anxiety traits and (B) autistic traits and metacognitive sensitivity, which was indexed by the area under the type 2 ROC curve (AUROC2). The blue line indicates the estimated linear relationship, with significant relationships being marked by an asterisk.

while the significant effect of zygomaticus activity hints towards a facilitating role of mimicry of smiles in emotion recognition, this link seems to be weakened with higher social anxiety traits. When examining the predicted value plot (see Fig. 5A), this effect, however, seems to be mainly driven by stronger variation in accuracies (i.e., also inaccurate responses) in individuals with lower social anxiety traits when the zygomaticus was not strongly activated. Otherwise, recognition of happy expressions was at ceiling and not much variation in relation to social anxiety trait levels could be observed.

Autistic traits. Similar to the models including social anxiety traits, there was no significant interaction between autistic traits and corrugator activity in accurately recognizing fearful or angry facial expressions (see Tables S15 and S17 in the Supplemental Material for the model fits). Contrasting the other negative expressions, the model on the recognition of sad expressions showed a significant interaction between corrugator activity and autistic traits as well as a significant main effect of corrugator activity. More specifically, in line with the social anxiety model, sad facial expressions were better recognized with higher corrugator activity, $\chi^2(1) = 4.556$, $p = 0.033$, $OR = 1.597$. This relationship was, however, weaker for higher autistic traits, interaction: χ^2 $(1) = 4.142$, $p = 0.042$, $OR = 0.668$ (see Fig. 5B and Table S18). Furthermore, significant effects of zygomaticus activity and of corrugator activity as well as a significant interaction between zygomaticus activity and autistic traits were found in the model on happy expressions, zygomaticus: $\chi^2(1) = 5.300$, $p = 0.021$, $OR = 14.184$, corrugator: $\chi^2(1) = 4.679$, $p = 0.031$, $OR = 0.069$, autistic traits*zygomaticus: $\chi^2(1) = 5.503$, $p = 0.019$, $OR = 0.137$. Thus, in addition to the activation of the zygomaticus, which was already described previously, a relaxation of the corrugator might facilitate the recognition of happy expressions. Similar to the model including social anxiety traits, autistic traits had a negative effect on the positive association between zygomaticus activity and accuracy in the recognition of happy expressions (see Fig. 5C and Table S16 in the Supplemental Material). This interaction again seemed to be driven by cases of low zygomaticus activity associated with inaccurate responses, but this time linked to low autistic trait levels.

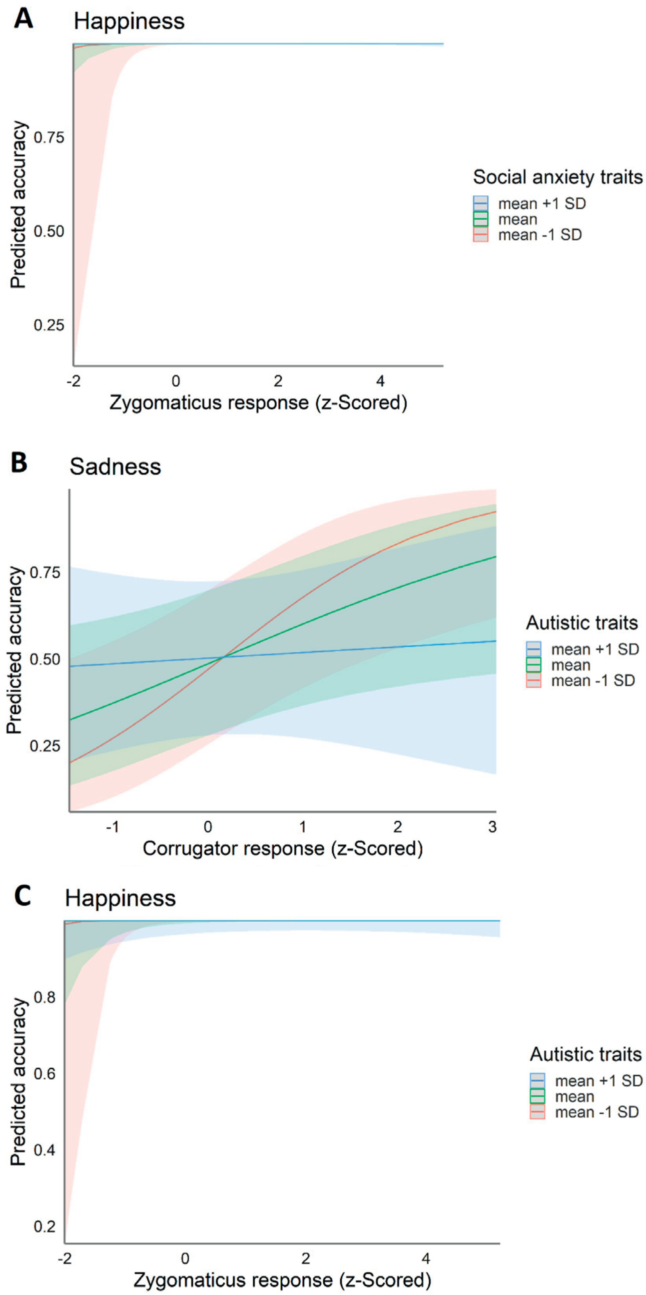


Figure 5. (A) The relationship between predicted accuracy in recognizing happy expressions and the corresponding filtered, baseline-corrected and z-scored zygomaticus activity depending on social anxiety trait levels. (B) The relationship between predicted accuracy in recognizing sad expressions and the corresponding filtered, baseline-corrected and z-scored Corrugator activity depending on autistic trait

levels. (C) The relationship between predicted accuracy in recognizing happy expressions and the corresponding filtered, baseline-corrected and z-scored zygomaticus activity depending on autistic trait levels. In the model fits, accuracy was coded binomial (0-1 values). For illustrative purposes, predicted accuracies for mean values as well as mean values +/- 1 SD of the continuous variables social anxiety traits and autistic traits are depicted. Shaded areas represent confidence intervals.

Discussion

In our study, we provided evidence that autistic traits and social anxiety traits are distinctly related to bottom-up (i.e., mimicry) and top-down (i.e., metacognition) components in emotion perception. Specifically, while individuals with higher social anxiety traits had significantly less confidence in their performance regarding all emotion categories, despite an unaltered actual emotion recognition performance, individuals with higher autistic traits were less accurate in the recognition of emotions, and in particular of fearful expressions. Furthermore, individuals with higher autistic traits seemed to be less able to calibrate their confidence judgments to their actual emotion recognition performance, as they displayed a poorer metacognitive sensitivity. Unexpectedly, we did not observe alterations in emotion-specific facial muscle mimicry with regard to either anxiety or autistic traits. Yet, we found indications that mimicry of frowning, indexed by corrugator activation, might facilitate the recognition of sad expressions, whereas mimicry of smiling, indexed by zygomaticus activation (and potentially relaxation of the corrugator), might support the recognition of happy expressions. Crucially, both links were less pronounced with higher autistic traits, while there was only weak evidence for a negative effect of social anxiety traits on the link between zygomaticus activity and accuracy in recognizing happy expressions.

Contradicting our expectations, we did not find a negativity bias (i.e., an improved recognition of negative expressions) with higher social anxiety traits reflected in our main analysis on the recognition accuracy of the displayed facial expressions. When using relative accuracy scores as an outcome (see Table S20 in the Supplemental Material), however, a better recognition of angry facial expressions with higher social anxiety trait levels could be observed. Given that an improved recognition of negative expressions in SAD was also not consistently found in the literature (Bui et al., 2017), the effect seems unstable and additional factors might play a role. For example, a heightened sensitivity to negative expressions in social anxiety (disorder) might only occur under brief exposure times or when actual interactions with the expresser could be expected (Staugaard, 2010). In this study, the presentation time was 2s and the participants were not engaged in any interaction. Effects related to biases in early visual attention (< 500ms) or to the fear of being negatively judged by an interaction partner were, therefore, highly unlikely. Importantly, social anxiety traits had the expected impact on the confidence judgment with regard to emotion recognition in our study. For all expression categories, confidence was reduced with higher social anxiety traits. The underconfidence in performance did, however, not affect the general positive link between confidence in emotion recognition and actual performance. Thus, while participants seemed to be able to calibrate their confidence ratings according to their recognition performance, a relative reduction in the confidence scores might have occurred with higher social anxiety traits. This observation might be a reflection of self-related negative beliefs about one's own social skills in high socially anxious people, which were likely formed in a public setting (Müller-Pinzler et al., 2019) and translated to a more global negative social skill assessment.

Theoretical models on SAD highlight low confidence in own social performance as a relevant cognitive bias in the development and maintenance of the disorder (Clark & Wells, 1995; Heimberg et al., 2010; Rapee & Heimberg, 1997). Evidence for this bias has been found in various studies contrasting social performance and subjective evaluations in real-life scenarios (Dijk et al., 2009; Kashdan & Savostyanova, 2011; Voncken & Bögels, 2008). The retrospective evaluation of one's performance in a social situation, so-called post-event processing, has been especially suggested to contribute to negative beliefs about one's social skills (Gkika et al., 2018). In both highly socially anxious individuals (Dannahy & Stopa, 2007) and individuals with a SAD diagnosis (Helbig-Lang et al., 2016), negatively-biased post-event processing has been shown to be more frequent, and positively related to social anxiety (symptoms). The lower confidence in emotion recognition associated with higher social anxiety traits in our study might also arise from doubts in one's own ability to recognize another person's emotional state correctly.

Facial muscle responses to emotional expressions were not found to be altered depending on social anxiety traits in our sample. This suggests that not only explicit emotion labelling but also implicit, automatic processes, namely facial mimicry, seem to be comparable across varying levels of social anxiety traits. In our study, there was also little evidence to assume that the link between facial muscle activity and emotion recognition accuracy would be modulated by social anxiety traits. The weakened positive association between zygomaticus responses and the accurate labelling of happy expressions with higher social anxiety trait levels in our study was most likely due to stronger variability in accuracies (i.e., also inaccurate responses despite close to ceiling performance overall) when zygomaticus activity was low. Additionally, the effect could not be reproduced in the analyses with relative accuracy as an outcome (see Supplemental Material). Taken our findings related to social anxiety traits together, heightened social anxiety trait levels were not associated with poorer emotion recognition performance or alterations in the link between facial mimicry and emotion recognition. Yet, confidence in emotion recognition was lower with higher social anxiety trait levels, which indicates that negative beliefs about one's skills might also exist in the domain of emotion recognition. In order to overcome this and other cognitive biases, Metacognitive Training can be a useful tool in the treatment of SAD (Nordahl & Wells, 2018).

In line with previous studies describing worse performance in emotion recognition tasks associated with ASD, we observed overall reduced accuracies with higher autistic traits, which became most apparent for fearful expressions (Frank et al., 2018; Sucksmith et al., 2013; Uljarevic & Hamilton, 2013). The recognition of sad expressions, on the other hand, was not as strongly affected by autistic traits in the main analysis, and even improved with higher autistic trait levels in the relative accuracy analysis (see Supplemental Material). This observation is compatible with a previous study, which reported a better recognition of sad facial expressions with higher autistic trait levels (C. Green & Guo, 2018). Confidence in recognizing displays of sadness as well as fear was rated higher with higher autistic traits. Neutral and happy facial expressions, in contrast, received lower confidence ratings with higher autistic trait levels. Given the negative impact of autistic trait levels on the recognition of fear displays, higher confidence ratings seem particularly surprising. The examination of the relationship between confidence and accuracy in emotion recognition (i.e., metacognitive sensitivity) revealed, however, that participants with higher autistic trait levels in our study were less able to scale their confidence according to their actual performance. Previous research on alterations in metacognitive judgments in ASD has already described a complex pattern of both over- and underconfidence in the social-cognitive domain (DeBrabander et al., 2020).

Our hypothesis that higher autistic trait level would result in reduced facial mimicry responses was also not confirmed. Even though we did not explicitly instruct participants to mimic, individuals with higher autistic trait levels seemed to automatically show unaltered facial muscle activation patterns, contradicting findings in clinical populations (McIntosh et al., 2006) as well as in healthy individuals with high autistic traits (Hermans et al., 2009). Importantly, it has been suggested that mimicry in ASD might especially be reduced for shorter presentation durations (Mathersul et al., 2013) and occur with a delay rather than not at all (Oberman et al., 2009), which we did not examine in our study. We did, however, observe a modulation in the link between facial mimicry and emotion recognition by autistic traits. In the recognition of sad expressions, increased activity of the corrugator, indicating mimicry of sadness, was less predictive of accurate recognition whereas the same applied to stronger zygomaticus activity in the recognition of happiness. While a sole evaluation of the latter effect would be difficult due to the ceiling performance in happiness recognition (see previous paragraph) as well as to a lack of reproducibility of a result when using a relative accuracy score (see Supplemental Material), the robust results concerning sadness recognition support the presence of a meaningful modulation.

It seems, thus, that facial mimicry plays a less informative role in emotion recognition, at least of sad expressions, in association with higher autistic trait levels. This observation is in line with past research that did not find an effect of automatic, intentional or externally induced mimicry on reports of the participant's own emotional experience in individuals on the autism spectrum, while neurotypical participants were considerably influenced by mimicry (Stel et al., 2008). According to the idea of the existence of two routes in emotion recognition, a fast one involving proprioceptive (bottom-up) information and a long one involving knowledge-based (top-down) information (Stel & van Knippenberg, 2008), the fast route might have been less employed in the recognition of sadness in participants with higher autistic traits. Since recognition performance of particularly sad expression was less negatively affected by higher autistic traits, judgments via the alternative, long route could have resulted in similarly successful judgments.

Previous studies have already reported qualitative differences in the recognition of sadness compared to other emotion expressions related to ASD. For example, recognition of sadness in static faces compared to point-light-displays has been found to be only improved in individuals with low but not with high autistic traits (Actis-Grosso et al., 2015). Moreover, while dynamic information (i.e., videos) generally improved emotion recognition for both autistic and neurotypical individuals, individuals on the autism spectrum recognized dynamic sad expressions worse compared to static ones (Enticott et al., 2014). Information that facilitates the recognition of sadness in neurotypical individuals might not serve individuals on the autism spectrum in the same way. Why this is specifically the case for sadness should be investigated in future studies.

Taken our findings related to autistic traits together, feedback from multiple sources might not be integrated beneficially in emotion recognition. On the one hand, confidence in emotion recognition does not seem to be scaled to actual performance. Internal feedback, in other words, the" feeling" how well one performed, might not be informative of actual performance in autism and, thus, cannot assist successful learning. Our findings suggest that, on the other hand, a simulation of observed expression might not be as informative for emotion processing in ASD compared to a neurotypical population. This claim is supported by research showing a reduced access to bodily signals (i.e., interoceptive accuracy) next to a heightened sensitivity to those signals in autism (Garfinkel et al., 2016), which seems to be driven by comorbid alexithymia (Ketelaars et al., 2016; Shah et al., 2016). Consequently, while interventions targeting metacognitive abilities could help overcome the gap between actual performance and subjective judgments in individuals on the autism spectrum, a training focusing on the integration of information from the bodily component of an emotional experience could indirectly benefit emotion recognition and other social skills.

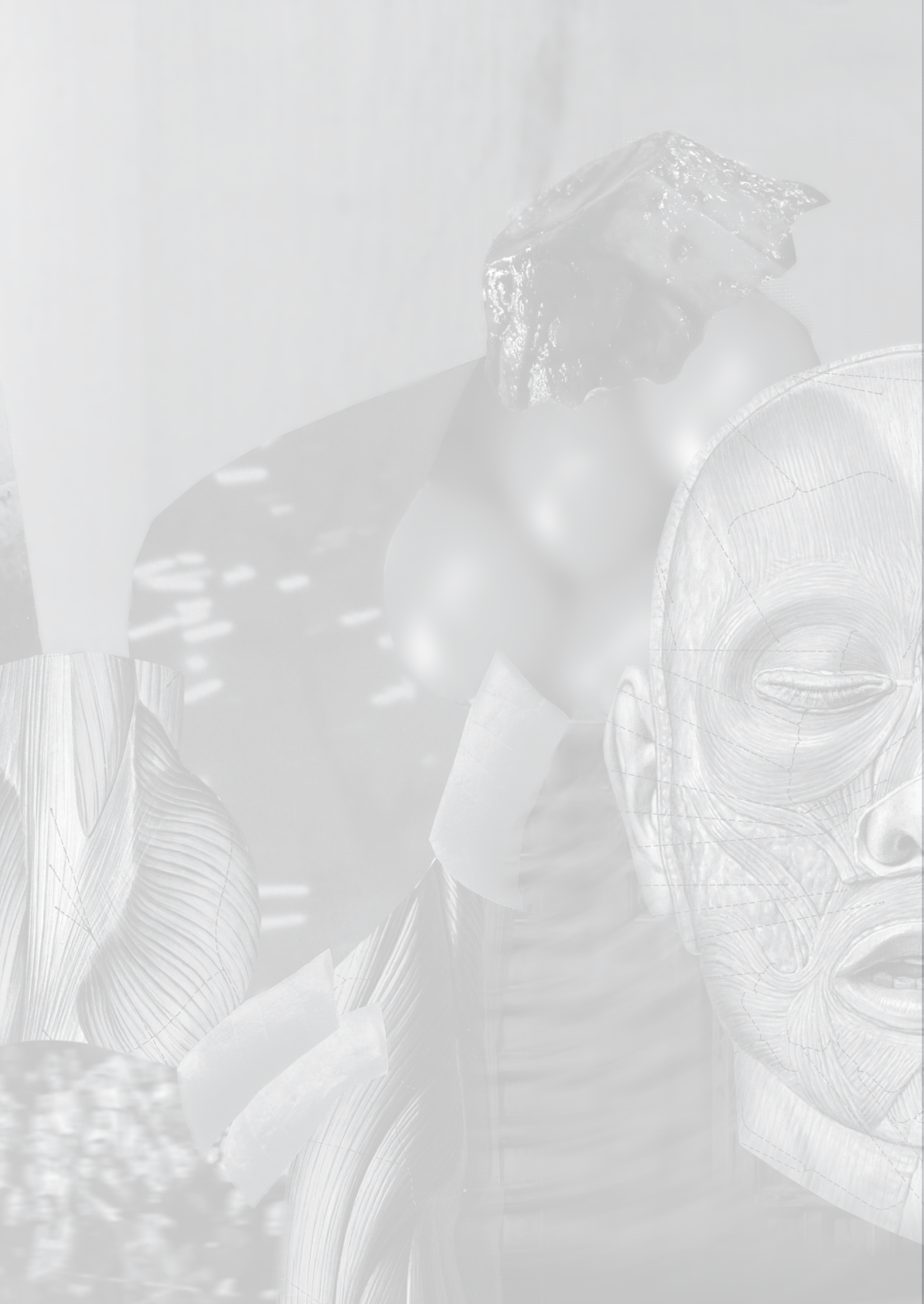
In addition to the results specific to the trait dimensions, our findings also add to the current discussion on the general role of facial mimicry in emotion recognition. Recent meta-analyses have described no robust relationship between facial mimicry and emotion recognition (Holland et al., 2020), as well as broader affective judgments (Coles et al., 2019). Our study, in contrast, revealed a link between facial mimicry responses to happy and sad expressions and associated recognition accuracy. More specifically, stronger activation of the zygomaticus and relaxation of the corrugator predicted better recognition of happiness, and stronger activation of the corrugator predicted better recognition of sadness. In some instances, sensorimotor simulation (i.e., activating facial muscle patterns that are congruent to observed emotional facial expressions) might indeed become a relevant mechanism in understanding others' emotions. Similar to previous literature, the effects were not robust in our study (see relative accuracy analysis in Supplemental Material), varied depending on clinical trait levels (see paragraphs above), and we did not observe significant relationships for all expression categories (e.g., not for anger). Our study therefore corroborates evidence that an embodiment of observed emotional expressions does not seem necessary for a successful recognition (Folz et al., 2022). Yet, facial feedback can become informative under certain conditions (Coles et al., 2019), and our results highlight that individual differences should additionally be considered.

Despite our efforts to create a more naturalistic emotion recognition scenario by displaying spontaneous, dynamic facial expressions of emotion, participants still observed standardized stimuli in a controlled lab setting in our study. This limits the generalizability of our results as the interpretation of emotional expressions has been shown to be highly context-dependent (Hess & Fischer, 2013; Israelashvili et al., 2019). In contrast to natural scenarios, the same stimuli were also presented repeatedly (three times) in different blocks. While the repeated presentation allowed us to obtain EMG responses without priming participants with emotion category words, learning effects might have occurred. For example, emotion recognition could have been facilitated or expressions could have been perceived as less intense. More importantly, our study did not involve a real social context. Without an interaction partner who receives and responds to expressions from the participant, the social communicative function of emotional expressions, including a bidirectional coordination of affective states (Keltner & Kring, 1998), may get lost (Schilbach et al., 2013). This limitation might also affect trait dimension-specific modulations in emotion perception. For example, in a real social situation, higher social anxiety levels have been associated with an enhanced mimicry of polite, but not enjoyment smiles (Dijk, Fischer, et al., 2018). Furthermore, ASD was argued to specifically become apparent in alterations in interpersonal dynamics (i.e., during bidirectional information exchange; see Bolis et al., 2018; Peper et al., 2016). Consequently, future studies on emotion perception should be conducted in real social situations that allow for reciprocity and affect coordination.

In addition to that, even though our observations on the impact of trait levels can give us hints with regard to alterations in clinical populations, we still collected data from a non-clinical sample. Once clinical symptoms that have a severe impact on an individual's life come into play, emotion processing might be altered differently, both qualitatively and quantitatively. Half of the participants in our sample had social anxiety trait levels that are considered clinically relevant (i.e., above 30; see Questionnaires section). While these high social anxiety trait levels for non-diagnosed individuals might result in findings that are comparable to clinical populations, this might be less applicable for our results regarding autistic traits. For example, while sadness recognition was observed to be least impacted by autistic trait levels in our study, a reduced perceptual sensitivity has been specifically described for sad facial expressions in individuals on the autism spectrum (Wallace et al., 2011). This emotion-specific recognition impairment has been shown to extend to difficulties in interpreting sadness from animations, which, in turn, has been related to worse daily social functioning in individuals on the autism spectrum (Boraston et al., 2007). Thus, in order to provide meaningful insights, results from studies including healthy participants with variations on clinical trait dimensions should always be confirmed in clinical populations as well as related to actual day-to-day experiences.

Moreover, while our sample was not gender-balanced, gender differences in mimicry and its integration in emotion recognition have been reported in past research (Dimberg & Lundquist, 1990; Stel & van Knippenberg, 2008), as well as in autistic traits and social anxiety traits (Caballo et al., 2014; Ruzich et al., 2015). Given the predominance of female participants in our sample, our findings cannot be easily generalized to the male population. Future studies should therefore examine whether similar effects to the ones described in the current study can be observed in a more balanced or even exclusively male sample. Lastly, as we did neither manipulate facial mimicry nor metacognition, our study does not allow for causality assumptions in their role in emotion recognition. Within an emotion processing context, information is likely to flow bidirectionally and recent findings support a context-dependent influence of emotion recognition on facial mimicry (Kastendieck et al., 2021). Furthermore, a more fine-grained investigation of potential mediatory processes in the course of emotion perception and interpretation, such as the integration of interoceptive information (Arnold et al., 2019; Critchley & Garfinkel, 2017a), might benefit the understanding of variability in emotion processing and enable the formalization of testable theoretical models (Smith et al., 2019).

In conclusion, our study provides evidence for distinct modulations of facial mimicry and metacognitive judgments in emotion recognition by autistic traits and social anxiety traits in a majorly female sample. Higher social anxiety traits were predominantly related to an underconfidence in emotion recognition, despite an unaltered performance, whereas higher autistic traits were associated with an overall worse recognition performance as well as a poorer calibration of performance judgments, and a less pronounced link between facial mimicry and emotion recognition. These trait dimension-specific patterns might also translate to the linked clinical disorders, which, however, still has to be confirmed in future studies. Importantly, particularities in processing others' emotions have been shown to contribute to social interactions difficulties experienced by individuals on the autism spectrum and by individuals with SAD. Hence, evidence-based interventions targeting condition-specific alterations in distinct components (i.e., metacognitive beliefs and bodily feedback) hold the promise to facilitate daily social encounters and improve the quality of life in the two clinical populations.



Chapter 5

Individual differences in interoception and autistic traits share altered facial emotion perception, but not recognition per se

Abstract

While alterations in both physiological responses to others' emotions as well as interoceptive abilities have been identified in autism, their relevance in altered emotion recognition is largely unknown. We here examined the role of interoceptive ability, facial mimicry, and autistic traits in facial emotion processing in non-autistic individuals. In an online Experiment 1, participants (*N* = 99) performed a facial emotion recognition task, including ratings of perceived emotional intensity and confidence in emotion recognition, and reported on trait interoceptive accuracy, interoceptive sensibility and autistic traits. In a follow-up lab Experiment 2 involving 100 participants, we replicated the online experiment and additionally investigated the relationship between facial mimicry (measured through electromyography), cardiac interoceptive accuracy (evaluated using a heartbeat discrimination task), and autistic traits in relation to emotion processing. Across experiments, neither interoception measures nor facial mimicry accounted for a reduced recognition of specific expressions with higher autistic traits. Higher trait interoceptive accuracy was rather associated with more confidence in correct recognition of some expressions, as well as with higher ratings of their perceived emotional intensity. Exploratory analyses indicated that those higher intensity ratings might result from a stronger integration of instant facial muscle activations, which seem to be less integrated in intensity ratings with higher autistic traits. Future studies should test whether facial muscle activity, and physiological signals in general, are correspondingly less predictive of perceiving emotionality in others in individuals on the autism spectrum, and whether training interoceptive abilities might facilitate the interpretation of emotional expressions.

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Data availability statement:

The datasets and materials generated and/or analysed during the current study will be made available on Dataverse NL upon publication: https://doi.org/10.34894/TOUSTD

Supplementary material:

Difficulties in recognizing others' emotions have been assumed to be one relevant source of broader social interaction difficulties in individuals on the autism spectrum (D. A. Trevisan & Birmingham, 2016; choice of autism terminology informed by Botha et al., 2023). Yet, recent research suggests a more differentiated picture: different paths to emotion recognition - rather than differences in ability- are likely to explain observed differences in emotion recognition between individuals on the autism spectrum and non-autistic individuals (Arnaud, 2020; Stel et al., 2008). For example, individuals on the autism spectrum might integrate their own mental representations of emotions less (Keating et al., 2023) and rather rely on learned rules when interpreting emotional expressions (Rutherford & McIntosh, 2007). One other path to emotion recognition draws on interoception, which involves the sensation of (changes in) physiological states (Craig, 2002). Via automatic alignment to an expressed emotion, or so-called emotional contagion (E. Hatfield et al., 1993; Prochazkova & Kret, 2017), physiological changes can not only inform an individual about their own emotional experience (Damasio, 1996) but can also offer insights in the emotional experience of others via simulation, such as facial mimicry (Wood et al., 2016). While previous research suggests that physiological responses to others' emotions (Davies et al., 2016; Hubert et al., 2009), as well as interoception (Garfinkel et al., 2016), would be altered in autism, little is known about the relevance of these alterations in an emotion recognition context. In the current study with a non-autistic sample, we aimed to approach a better understanding of the role of physiological signals and their sensation in emotion recognition alterations in relation to autistic trait levels paving the way for future investigations in autism..

The Body in Emotion Perception in Autism

Past studies on the recognition of facial or bodily emotion expressions in autism predominantly report worse performance, that is, a lower sensitivity to emotions or less accuracy in labelling them, compared to non-autistic samples (Frank et al., 2018; Uljarevic & Hamilton, 2013). Individuals on the autism spectrum have further been shown to differ from non-autistic individuals in their physiological responses to observed emotional expressions. More specifically, both hyper- and hypoarousal to emotion displays have been reported (Cuve et al., 2018; Hubert et al., 2009), whereas the automatic mirroring of facial expressions (i.e., facial mimicry) has typically been found to be reduced (Davies et al., 2016). Facial mimicry patterns are thought to play an important role in attributing discrete emotions to facial expressions, as they are specific for different emotion categories (Folz et al., 2022; Wingenbach et al., 2020) and can act as simulations of observed expressions (Arnold & Winkielman, 2020; Wood et al., 2016). Robust evidence for a link between facial mimicry and emotion recognition has not been established in the scarce literature on this topic (Holland et al., 2020). Yet, some studies have found that non-autistic individuals were influenced by their own facial expressions in attributing emotional states to themselves (Soussignan, 2002; Stel & van Knippenberg, 2008) and others (Drimalla et al., 2019; Sato et al., 2013). In contrast, no influence of facial mimicry on experienced emotions, even if it was intentionally produced, has been reported in individuals on the autism spectrum(Stel & van Knippenberg, 2008). Furthermore, in non-autistic samples, reduced facial mimicry has, if at all, only been linked to higher autistic trait levels for very specific emotions and subgroups (Hermans et al., 2009). Interestingly, in our recent study in which no systematic modulations of facial mimicry by autistic trait levels have been found, a weaker link between facial mimicry responses to sad facial expressions (i.e., mirroring of frowns) and successful emotion recognition has been observed (Folz et al., 2023). Thus, the presence of physiological alignment to emotional expressions might not be sufficient to facilitate emotion recognition. In order to integrate information about one's own physiological state in emotion processing, certain interoceptive abilities, namely an awareness of changes in physiological state as well as an accurate representation thereof, may be necessary. Findings from various studies support the link between emotional and somatic awareness, with the latter being more fundamental (Kanbara & Fukunaga, 2016). Hence, in the current study we aimed to identify whether individual differences in the sensation and integration of one's physiological signals would be linked to emotion recognition outcomes, and whether this could offer an explanation to altered emotion processing associated with variations in autistic trait levels.

Interoception in Emotion Processing

Research on interoception, or the "sense of the physiological condition of the entire body" (Craig, 2002), has recently highlighted the integration of physiological signals in central processing beyond homeostatic control, widely influencing human cognition and behaviour (Critchley & Harrison, 2013). This also entails the affective domain (Critchley & Garfinkel, 2017). By detecting and assigning meaning to physiological changes, interoceptive processes can become an important mechanism in emotion processing (Smith & Lane, 2015). From a predictive coding perspective, emotional states have even been suggested to arise from active inference of causes of physiological changes (Seth, 2013). If, for example, various afferent interoceptive signals indicate a state of heightened physiological arousal, the mismatch to a predicted calmer state is resolved by acquiring more sensory information about likely internal and external causes, with their integration in updated models resulting in an emotion percept. Importantly, individuals vary in the processing of interoceptive input at different levels in the hierarchy (Suksasilp & Garfinkel, 2022), and various measures have been developed to assess these individual differences. In a common interoception model (Garfinkel et al., 2016), three interoceptive dimensions are distinguished (Forkmann et al., 2016; Garfinkel et al., 2015), namely interoceptive accuracy (i.e., the objective accuracy in the detection of interoceptive signals), interoceptive sensibility (i.e., the self-reported, subjective tendency to focus and be aware of interoceptive signals) and interoceptive awareness (i.e., the ability to assess one's interoceptive accuracy correctly, i.e. a metacognitive process). Next to these dimensions, the correspondence between interoceptive sensibility and accuracy, the so-called interoception trait prediction error (Garfinkel et al., 2016), can provide valuable information about the mismatch between subjective beliefs and objective measures. The scope of this model in describing subjective beliefs is limited as it fails to distinguish between beliefs regarding accuracy in perceiving interoceptive signals versus attention to them. To capture this dissociation, Murphy et al. (2019) developed a 2x2 factor model of interoceptive ability, with the first factors ('What is measured?') distinguishing between accuracy and attention. The second factor ('How is it measured?') contrasts beliefs regarding one's accuracy/attention (i.e., self-reports) with one's actual behaviour regarding the two targets (i.e., objective measures).

Most research in the field of emotion processing has employed objective task-based interoception measures, which contrast the (objectively measured) nature of a specific afferent signal (e.g., timing, strength) to its subjective experience. The firing of baroreceptors has been highlighted as afferent signal in the cardiovascular domain, among other signals (Desmedt et al., 2023), indicating cardiovascular arousal in emotion processing (Critchley & Garfinkel, 2017). In frequently used cardiac interoception tasks, participants either keep track of their heartbeats within a specific time window (i.e., heartbeat counting) or judge the synchronicity of their heartbeats with auditory information (i.e., heartbeat discrimination). Even though these tasks were designed to provide insights in the subjective experience of afferent cardiac signals, they are not exclusively reflecting the accurate perception of cardiac interoceptive signals The heartbeat discrimination task, for example, further requires participants to match the subjective experience of the heartbeat timing to the timing of an external stimulus. Diverging task demands might thus also explain the relatively low correspondence between different measures of cardiac interoceptive accuracy (Hickman et al., 2020). Interoceptive accuracy can be assessed in various bodily systems (i.e., domains; Murphy et al., 2018), and performance on objective interoceptive accuracy measures in these distinct domains (e.g., cardiac, respiratory) differs within individuals (Garfinkel et al., 2016).Self-report measures on interoceptive accuracy, as described in the 2x2 factor model, aim to assess the accurate perception of interoceptive signals across domains (referred to as "trait interoceptive accuracy" in the following; Murphy et al., 2019). The Interoceptive Accuracy Scale requires participants to rate the degree to which their subjective experience of several afferent signals each relate to actual physiological needs. Indicators for evaluating the accurate perception of sensations can be quite diverse, with actually vomiting (when feeling the urge to vomit) or being full (after giving in to hunger) as examples. Although this multifaceted measure of interoceptive accuracy may capture not only interoception but also subjective beliefs and experiences in everyday life, there is evidence that it would correspond to cardiac interoceptive accuracy (Murphy et al., 2020).

In previous research on the role of interoception in emotion processing, individuals with higher cardiac interoceptive accuracy have not only been found to show stronger physiological responses (Pollatos & Schandry, 2008) and report more intense emotional experiences (Dirupo et al., 2020; Wiens et al., 2000) when viewing emotional images, but the link between their physiological changes and their subjective arousal levels has also been reported to be stronger (Dunn et al., 2010). This is in line with the suggestion that individuals with high objective interoceptive accuracy would be able to increase the precision of their interoceptive prediction errors relative to their interoceptive priors, and also to other sensory modalities, via attentional processes (Ainley et al., 2016): once physiological changes are detected and propagated in an emotional context, individuals with higher objective interoceptive accuracy should show stronger autonomic responses to emotional stimuli , (i.e., a reinforcement via active inference) as bottom-up interoceptive information should have a stronger influence on information processing. Higher cardiac interoceptive accuracy has further been related to a better recognition of negative emotional expressions (Fittipaldi et al., 2020; Terasawa et al., 2014), supporting the idea that an accurate representation of interoceptive information might also facilitate recognizing emotional states of others. The few studies examining the role of interoceptive sensibility in emotion processing have also mainly observed a facilitation of processing, such as faster emotion recognition (Hübner et al., 2021) and a more precise adaption to emotion probabilities (Hübner et al., 2021, 2022). Yet, links might be specific to different subcomponents of interoceptive sensibility (Desdentado et al., 2022) as well as depend on the task at hand (Ventura-Bort et al., 2021). Overall, individuals with a less accurate representation of interoceptive signals or a lower tendency to monitor them might not benefit from their integration in emotion recognition, as it might be the case in autism.

Interoception in Autism

Alterations in interoception have been associated with various physical, neurodevelopmental and mental health conditions (Bonaz et al., 2021; Khalsa et al., 2018), including autism (DuBois et al., 2016; Proff et al., 2022). Compared to non-autistic control samples, many studies have found a reduced interoceptive accuracy in adults (Failla et al., 2020; Garfinkel et al., 2016; Mul et al., 2018) and children (Failla et al., 2020; Nicholson et al., 2019) on the autism spectrum. Worse performance in interoceptive accuracy tasks could, however, not consistently be observed in both populations (Nicholson et al., 2019; Schauder et al., 2015), and also when using different tasks (Z. J. Williams et al., 2023). Studies examining the subjective experience of interoceptive signals (i.e., sensibility) are similarly inconsistent: studies have found increased sensibility (Garfinkel et al., 2016; Pickard et al., 2020), reduced sensibility (Mul et al., 2018) or no differences between individuals on the autism spectrum and non-autistic individuals (Butera et al., 2023). Different study populations as well as measurement tools might explain inconsistencies. Questionnaires focusing on the sensation of specific body signals, such as the Body Perception Questionnaire (Porges, 1993), might be reflective of the hypersensitivity to interoceptive signals that individuals on the autism spectrum can experience. This increased interoceptive sensibility has been found to strongly diverge from a decreased interoceptive accuracy in individuals on the autism spectrum, resulting in a relatively higher interoceptive trait prediction error (Garfinkel et al., 2016). In contrast, questionnaires focusing on a more global awareness, integration or interpretation of signals, such as the Multidimensional Assessment of Interoceptive Awareness (Mehling et al., 2018), might rather be reflective of the difficulty to make sense of bodily signals. In order to capture these subjectively experienced difficulties in individuals on the autism spectrum, the Interoception Sensory Questionnaire was developed as assessment tool for "interoceptive confusion". Here, interoceptive confusion has not only been found to be highly prevalent in individuals on the autism spectrum, but also increasing in severity the higher an individual's autistic trait levels in a non-autistic population (Fiene et al., 2018). These findings are in line with predictive coding theories on interoception in autism (Quattrocki & Friston, 2014; van de Cruys et al., 2014) which suggest that individuals on the autism spectrum would be hypersensitive to interoceptive signals, overrepresent them at low processing levels (i.e., distinct sensations) and have a reduced accuracy in their sensation due to highly precise and inflexible prediction errors, while the integration of signals to a global awareness might be constrained. As previously outlined, somatic awareness might build an important foundation for emotional awareness with regard to both our own and others' emotions (Kanbara & Fukunaga, 2016). Thus, sensing interoceptive signals less accurately or integrating them to a lesser degree could potentially explain differences in emotion recognition tasks that are observed between non-autistic individuals and individuals on the autism spectrum, or related to high autistic trait levels.

The Role of Interoception in Processing Others' Emotions in Autism

Only few studies have investigated the role of interoception in processing others' emotions in autism. Focusing on (emotional) empathy as an outcome, two recent studies comparing individuals on the autism spectrum to non-autistic individuals have shown inconsistent findings: While no group differences in interoceptive sensibility measures, as well as no link to emotional empathy, have been observed in one study (Butera et al., 2023), the other study has found both reduced interoceptive sensibility and cardiac interoceptive accuracy in autism, with the latter showing a negative relation with empathy (Mul et al., 2018). Importantly, both studies have highlighted the relevance of co-occurring alexithymia, a trait encompassing difficulties in identifying and describing one's emotions (Nemiah et al., 1976), in explaining the link between altered interoceptive processing and potential difficulties in empathy related to autism. Alexithymia has consistently been linked to difficulties in emotion recognition (Jongen et al., 2014; Lane et al., 1996; Parker et al., 1993) and shows a high prevalence in autism (49.93%; Kinnaird et al., 2019). Studies assessing alexithymia levels in individuals on the autism spectrum provide evidence that alterations in various aspects of emotion processing in autism (Gaigg et al., 2018; Ketelaars et al., 2016), as well as in interoceptive ability (Shah et al., 2016), might indeed be explained by co-occurring high alexithymia levels. Yet, whether a reduced subjective and/ or objective interoceptive accuracy would account for difficulties in emotion recognition related to autism remains an open question. In contrast to this potential consequences of a reduced interoceptive accuracy, The heightened interoceptive sensibility in autism, reflecting a hypersensitivity to (specific) bodily signals, has been linked to more severe autism symptomology in specific domains, namely to socio-affective features in children (Palser et al., 2020) as well as to a reduced emotion sensitivity and the occurrence of anxiety symptoms in adults on the autism spectrum (Garfinkel et al., 2016). Thus, learning to regulate and optimally integrate interoceptive information might benefit individuals on the autism spectrum in their daily (social) functioning and experiences. While the amount of literature on clinical interventions in autism focusing on attention to and integration of physiological signals is growing (Gaigg et al., 2020; Quadt et al., 2021), the role of altered interoceptive processing in autism symptomology, including the socio-affective domain, is still scarcely investigated.

Individual characteristics associated with autism can be observed in the general population to varying degrees, resulting in claims that individuals on the autism spectrum could be positioned at the extreme of a continuum of autistic traits (Constantino & Todd, 2003; Robinson et al., 2011). This perspective received support by genetic studies (Bralten et al., 2018; Lundström et al., 2012) as well as studies focusing on behavioural aspects of autism (Mayer, 2017). Accordingly, non-autistic individuals with higher autistic trait levels show, in some regards and to some extent, similar patterns of alterations in processing observed emotional expressions as individuals on the autism spectrum (Åsberg Johnels et al., 2017; Folz et al., 2023; Hermans et al., 2009). Importantly, findings on links between autistic trait levels in non-autistic samples and certain outcomes of interest cannot simply be generalized to autism, let alone to experiences of individuals on the autism spectrum (Sasson & Bottema-Beutel, 2022). They can, however, help forming assumptions on which factors, within processes that show similar patterns of alterations in autism and high autistic trait levels, might be relevant to further examine in autism (Pollmann et al., 2010).

Objectives of the Current Study

We investigated the role of interoception and facial mimicry in emotion processing in relation to autistic trait levels in two pre-registered experiments with non-autistic individuals (see Figure 1): The first, online experiment consisted of a facial emotion recognition task with confidence judgments in the accuracy of recognition and intensity ratings of seen expressions as well as questionnaires on autistic traits, trait interoceptive accuracy and interoceptive sensibility. Social anxiety traits and alexithymia were assessed as control variables given that both have been related to alterations in interoception (Desai et al., 2019; Stevens et al., 2011), as well as difficulties in the socio-affective domain in autism (Mul et al., 2018; Spain et al., 2018). In our main analysis, we examined whether a reduced trait interoceptive accuracy would explain a reduced emotion recognition accuracy with higher autistic trait levels, while controlling for alexithymia and social anxiety traits. In the second, lab-based experiment, we expanded the online study. Next to assessing the same measures as in the online experiment for replication purposes, we added facial electromyography recordings during the emotion recognition task. This allowed us to investigate a second factor which could play a role in reduced emotion recognition with higher autistic trait levels: We tested whether physiological responses to others' facial expressions (i.e., facial mimicry) were less predictive of emotion recognition accuracy with higher autistic trait levels as found in a previous study for sad facial expressions (Folz et al., 2023). By adding a heartbeat discrimination task to the lab experiment, we could further explore whether autistic traits would be linked to lower cardiac interoceptive accuracy and/or a stronger mismatch between subjective and objective measures of interoception (interoceptive trait prediction error).

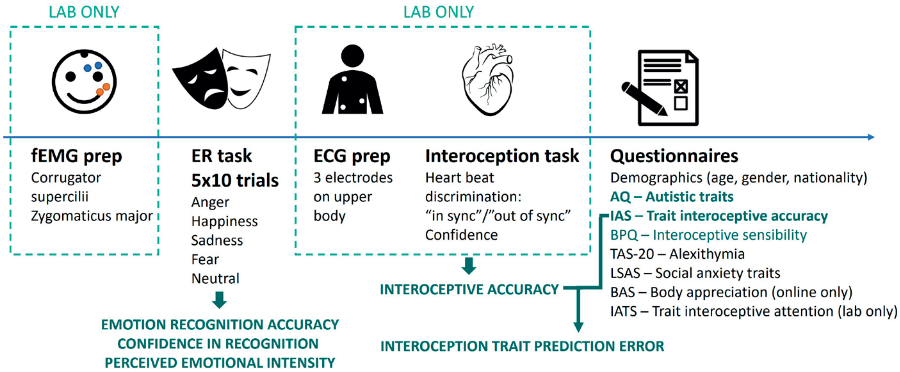

Figure 1. Experimental design of the online study (Experiment 1) and the lab study (Experiment 2. prep = preparation, fEMG = facial electromyography, ER = emotion recognition, ECG = electrocardiography, AQ = Autism Quotient, IAS = Interoceptive Accuracy Scale, BPQ = Body Perception Questionnaire, LSAS = Liebowitz Social Anxiety Scale, TAS-20 = Toronto Alexithymia Scale (20-item version), BAS = Body Appreciation Scale (not examined), IATS = Interoceptive Attention Scale.

Experiment 1

Method

Participants

We tested 100 adult participants between 18-35 years-old who reported no prior or current psychiatric or neurological disorder. The choice of the sample size was based on a power analysis with simulated data, indicating a power of .94 (or 1) to find significant relations between autistic traits (or social anxiety traits) and emotion recognition accuracy with a similar effect size as in a previous study (Folz et al., 2023). More details on the sample size rationale can be found in the preregistration of the study (https://osf.io/wugq7). Out of the 100 participants, 70 participants were recruited via the online recruitment platform SONA of Leiden university (student population) and 30 participants were recruited via a direct link between 28/12/2020 and 24/01/2021. One participant did not meet the age criterion (18-35 years-old) and was excluded after data collection. Our final sample consisted of 99 participants (86 females, 12 males, 1 'prefer not to say') with an age range between 18 and 34 years (M = 21.39, SD = 4.27). The majority of our participants were Dutch (45 individuals), Macedonian (23 individuals) or German (10 individuals), and all participants completed the experiment in English. There was no direct monetary reimbursement for participation. Yet, all participants could enter a lottery (10% chance of winning) to either receive a 10€ vouchers for an online store in the EU or to donate 10€ to 'Give Well' charity (https://www.givewell.org/). Leiden university students could additionally receive 2 course credits. All participants provided informed consent prior to participation. The study was conducted according to the Declaration of Helsinki and the protocol was approval by the local ethics committee of the Faculty of Social and Behavioural Sciences at Leiden University (2020-12-18-M.E. Kret-V1-2834).

Stimuli

Color videos of 5 male and 5 female individuals, showing spontaneous facial expressions of anger, happiness, fear, sadness and neutral in full frontal view, were selected from a previous standardization (Folz et al., 2023) of the FEEDTUM stimulus database (Wallhoff et al., 2006). All videos had a length of 2s (500ms neutral expression followed by 1500ms expression of the respective category) and a gray background. The size of the videos was automatically adjusted to the participants viewport size (4: 3 ratio). All participant viewed all 50 videos once in a random order.

Procedure

The experiment was performed on the online experiment platform Gorilla (Anwyl-Irvine et al., 2020) (https://gorilla.sc/). Participants were instructed to complete it on a PC screen in a quiet room, without any disturbances. As first part of the experiment, participants performed an emotion recognition task. Each trial started with a central fixation cross for 1s. Afterwards, a facial expression video (see Stimuli section) was presented in the centre of the screen for 2s and followed by a 100ms blank screen. On the next screen, participants chose a label for the displayed expression ('Which type of expression was displayed by the person in the video?') out of the 5 potential categories (angry/happy/sad/fearful/neutral). They additionally rated the confidence in their decision ('How confident are you about your decision?') on a visual analogue scale from "not confident at all' to 'very confident'. Integer values ranged from 0-100 but were not visible to the participant. As last rating on the same screen, participant indicated the perceived emotional intensity of the expression ('How emotionally intense was the expression displayed in the video?') on a visual analogue scale from 'not intense at all' to 'very intense'. Integer values again ranged from 0-100 but were not visible to the participant. Participants could move on to the next trial in a self-paced manner once all three questions had been answered. After the emotion recognition task, all participants provided demographical information regarding their age, gender, and nationality first. The order of the following questionnaires (see Measurements section and Figure 1) was randomized across participants. At the end of the experiment, participants could decide to enter the lottery for the 10€ vouchers/donation by providing their email address.

Measurements

Autistic traits. We used the Autism-Spectrum Quotient (AQ; Baron-Cohen et al., 2001) as a self-report measure of traits associated with the autism spectrum. Respondents rate how strongly each of 50 items applies to them on a 4-point Likert scale (1 = definitely agree, 2 = slightly agree, 3 = slightly disagree, and 4 = definitely disagree). Some items are reverse-coded, and all items scores are binarized (1 or 2 to 0 and 3 or 4 to 1) before summation. Sum scores can be calculated for five separate subscales with ten items each (social skill, attention switching, attention to detail, communication, and imagination) as well as for one total autistic trait score. Higher sum scores reflect higher autistic trait levels. In our experiments, 2 participants had a higher AQ score than 32 which has been described as cut-off for clinical significance. More detailed descriptive information about all questionnaires scores, including an overview of the reliabilities and distribution parameter, can be found in Table 1. A visualization of the relations between the questionnaire measures can be found in Figure S1A in the Supplemental Materials.

Trait interoceptive accuracy. The Interoceptive Accuracy Scale (IAS; Murphy et al., 2020) was used to assess self-reported interoceptive accuracy with regard to various body sensations (e.g., heartbeat, hunger, need to urinate,..). Interoceptive accuracy for each of the 21 IAS-items are evaluated on a 5-point Likert scale (1 = disagree strongly, 2 = disagree, 3 = neither agree nor disagree, 4 = agree, and 5 = strongly agree), and higher sum scores represent a higher self-reported interoceptive accuracy (see Table 1).

Interoceptive sensibility. We used the body awareness scale of the short form of the Body Perception Questionnaire (BPQ-SF; Porges, 1993) to assess interoceptive sensibility in our sample. Statements regarding the awareness of 26 body sensations (e.g., sweaty palms, stomach and gut pains,..) are rated on a 5-point Likert scale (1 = never, 2 = occasionally, 3 = sometimes, 4 = usually, and 5 = always). Sum scores are regarded as an integrated measure of interoceptive sensibility, with higher scores indicating higher interoceptive sensibility (see Table 1).

Alexithymia. With the 20 item version of the Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994), we assessed alexithymia in our sample. Each item of the TAS-20 is rated on a 5-point Likert scale from 1 (strongly disagree) to 5 (strongly agree), with five items being reversely coded. The items can be summarized on three subscales ("Difficulty identifying feelings", "Difficulty describing feelings", "Externally-oriented thinking") as well as summed to a total score, with a higher score higher alexithymic trait levels. Total scores were higher than 61 for 10 participants (10%), indicating alexithymia (see Table 1).

Social anxiety traits. The Liebowitz Social Anxiety Scale (LSAS; Liebowitz, 1987) was used to assess self-reported social anxiety traits. Respondents rate their fear and avoidance in 24 social interaction and performance separately on 4-point Likert scales (fear: 1 = None, 2 = Mild, 3 = Moderate, 4 = Severe; avoidance: 1 = Never, 2 = Occasionally, 3 = Often, 4 = Usually). In our sample, 65 participants (66 %) exceeded the theoretical cut-off of 30 which indicates a probability of social anxiety disorder, with 26 participants (26%) scoring high (above 60) on this scale (see Table 1).

Body appreciation. As part of a Master thesis project, participants also completed the updated version of the Body Appreciation Scale (BAS-2; Tylka & Wood-Barcalow, 2015). The results were not of interest to answer the research question of this article and are therefore not reported.

Table 1. Distribution of Questionnaires Scores, Including their Internal Consistency (Cronbach's Alpha) and Distribution Parameters, in the Online Study (Experiment 1)

	N	Mean	SD	Min	Max	α	lCL	hCL	kurtosis	skewness
AQ	99	17.05	6.59	3	34	0.79	0.73	0.85	2.89	0.37
IAS	99	79.80	9.25	51	100	0.82	0.77	0.87	2.97	-0.20
BPQ	99	72.48	25.16	26	126	0.96	0.95	0.97	2.00	0.15
LSAS	99	44.00	23.88	0	117	0.96	0.94	0.97	3.09	0.71
TAS	99	45.22	11.28	24	73	0.85	0.81	0.89	2.23	0.34

Note. AQ = Autism Quotient (Autistic traits), IAS = Interoceptive Accuracy Scale (Trait interoceptive accuracy), BPQ = Body Perception Questionnaire (Interoceptive sensibility), LSAS = Liebowitz Social Anxiety Scale (Social anxiety traits), TAS = Toronto Alexithymia Scale (Alexithymia), lCL/hCL = lower/higher Confidence Level of 95% Confidence Interval associated with α.

Data Analysis

We preregistered the data analyses to test our hypotheses on the Open Science Framework (https://osf.io/wugq7). The data of the two experiments was collected at different stages of the Covid-19 pandemic. Since this might have resulted in biased replies on the social anxiety trait measure, which included, for example, questions about avoidance of social situations, we decided to focus on *Autistic traits* as the main predictor in our analyses, which were all conducted in R 4.2.2 (R Core Team, 2022) . As preregistered, interactions between *Social anxiety traits* and *Emotion category* were still included in all clinical-trait-score-related analyses as control predictors, similar to *Alexithymia*. The two clinical trait score measures showed to have significant medium positive correlations with one another, as well as with *Alexithymia* (LSAS-AQ: $r_s = 0.47, p < .001$; LSAS-TAS: $r_s = 0.34, p < .001$; AQ-TAS: $r_s = 0.30, p = .003$), supporting our approach to control for *Social anxiety traits* and *Alexithymia* in all models. Before fitting our models, all continuous variables were standardized (i.e., centered and scaled) to obtain standardized beta coefficients. In order to test whether trait interoceptive accuracy would (partially) mediate the link between autistic trait levels and emotion recognition accuracy, we fitted three models using the lmerTest package (Kuznetsova et al., 2017): First, we tested whether emotion recognition accuracy was decreased with higher autistic trait levels (path c) while controlling for social anxiety traits and alexithymia. Previous literature has reported emotion-specific alterations in recognition performance with regard to autistic traits, but also with regard to social anxiety traits. Therefore, the binary outcome *Emotion recognition accuracy* (1= correct, 0 = incorrect) was predicted by a two-way interaction between *Emotion category* (angry, happy, fearful, sad and neutral) and *Autistic traits* as well as by a two-way interaction between *Emotion category* and *Social anxiety traits*, and *Alexithymia* as control predictors. Random intercepts for each stimulus (50 stimuli) as well as for each participant (99 participants) were added. After model fitting, slopes for the relation between *Autistic traits* and *Emotion recognition accuracy* were estimated for each level of *Emotion category*, using the emtrends function of the emmeans packages(Lenth, 2023; Holm method for p-value adjustment). Second, we examined whether *Trait interoceptive accuracy* was reduced with higher *Autistic traits* levels (path a), while controlling for *Social anxiety traits* and *Alexithymia*. A linear regression analysis was performed with *Trait interoceptive accuracy* as outcome variable and *Autistic traits* as predictor of interest, as well as *Alexithymia* and *Social anxiety traits* as control predictors. In the third and final model fit, we added an interaction between

Emotion category and *Trait interoceptive accuracy* as a mediator of the association between *Autistic Traits* and *Emotion Recognition*, next to the predictors in the first model, to be able to identify whether the effect of *Autistic traits* on *Emotion recognition accuracy* for certain levels of *Emotion Category* was mediated by *Trait interoceptive accuracy* (path ab). The causal mediation model was tested using the RMediation package (Tofighi, 2023). From the previously defined models, path a was defined as the effect of *Autistic traits* on *Trait interoceptive accuracy* and path b as the effect of *Trait interoceptive accuracy* on *Emotion recognition accuracy* of expression(s) that were less well recognized with higher autistic trait levels. The indirect effect (path ab) of *Trait interoceptive accuracy* on the association between *Autistic traits* and *Emotion recognition accuracy* of (certain) emotional expressions was also tested for significance.

We further explored the role of both autistic traits as well as self-reported interoception measures in determining the two other emotion recognition task outcomes, namely confidence in emotion recognition and perceived emotional intensity of seen expressions. As we did not expect the variables to influence each other in predicting the outcomes and aimed to avoid inflation of type I error, all predictor variables were included in one mixed model for each outcome. *Perceived emotional intensity* was thus predicted by two-way interactions between *Emotion category* and *Autistic traits*, *Emotion category* and *Trait interoceptive accuracy,* and *Emotion category* and *Interoceptive sensibility* as well as by the two-way interaction between *Emotion category* and *Social anxiety traits,* and *Alexithymia* as control predictors. In line with the *Emotion recognition accuracy* models, random intercepts for each stimulus and each participant were added. The distribution of the confidence data was not normal and the highest value (100) was selected in many trials (20%), indicating full confidence. Therefore, we fitted a Bayesian GLMM, using the brms package (Bürkner, 2017), with a zero-one-inflated family instead of a LMM to predict *Confidence in emotion recognition* with the same random and fixed effect structure as the intensity model. Thus, we estimated separate parameters for a beta regression excluding zeros and ones (phi), for the proportion of zeros and ones only (zoi) as well as for the proportion of ones versus zeros (coi). Integrated posterior estimates for the slopes at three different values of the predictors of interest (-1, 0, 1) were obtained using the emtrends function of the emmeans package. All visualizations of effects and all model fit tables are based on the sjPlot package (Lüdecke, 2021).

As additional analyses, we explored relations between *Autistic traits* and *Interoceptive sensibility* as well as between *Interoceptive sensibility* and *Emotion recognition accuracy*. As no significant effects related to autistic trait levels were observed and these analyses were exploratory, the models are reported in the Supplemental Materials (see Tables S10 - S12) and not discussed in detail here.

Results

Main Analysis

We did not find evidence for trait interoceptive accuracy mediating the effect of autistic traits on emotion recognition (see Figure 2). As only recognition of angry expressions showed to be worse with higher autistic trait levels, (**path c,** see Figure 4A and Table 2 for the slope comparisons, as well as Table S1 in the Supplemental Materials for the full model fit), we tested for an indirect effect of *Trait interoceptive accuracy* on the association between *Autistic Traits* and *Emotion recognition accuracy* of angry expressions (**path ab**). Confidence limits included zero, indicating no mediated effect (see Figure 2). Thus, autistic traits predicted worse recognition of angry faces only directly. Against our expectations, *Autistic traits* was not a significant predictor of *Trait interoceptive accuracy* in our second model (**path a,** see Table S3 in the Supplemental Material), and neither *Trait interoceptive accuracy* nor its interaction with *Emotion category* were significant in predicting *Emotion recognition accuracy* (**path b,** see Table S5 in the Supplemental Material). An exclusion of *Alexithymia* from all models including *Autistic traits* as predictor did not result in a meaningful change of the outcomes. All model fits, including significant effects that are unrelated to our predictors of interest, can be found in Tables S1-5 in the Supplemental Materials.

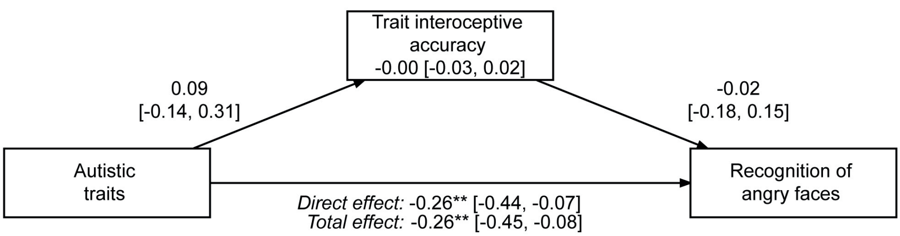

Figure 2. Results of the mediation analysis in Experiment 1 with trait interoceptive accuracy as potential mediator explaining worse recognition of angry faces with higher autistic trait levels. ** p < .001

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Table 2. Estimated Slope of the Linear Relation Between Autistic Traits and Emotion Recognition by Emotion Category, and Results of the Slope Comparisons against Zero

	Estimated slope [SE]	95% CI	z-ratio	p-value
Emotion category				
Angry	-0.30 [0.11]	-0.58, -0.02	-2.78	.027
Fearful	0.02 [0.13]	-0.31, 0.36	0.18	1
Happy	-0.03 [0.21]	-0.57, 0.51	-0.16	1
Sad	-0.02 [0.10]	-0.28, 0.24	-0.18	1
Neutral	0.14 [0.11]	-0.15, 0.43	1.22	.895

Note. Confidence intervals are adjusted for multiple comparisons using the Bonferroni-method, and p-values are adjusted using the Holm-method.

Exploratory Analyses

In the model with *Perceived emotional intensity* as an outcome, we did not find an effect of *Autistic traits* (neither as main effect nor as interaction with *Emotion category*). While the interaction between *Trait interoceptive accuracy* and *Emotion category* was significant (see Figure 4C), $F(4,4786) = 3.28$, $p = .011$, the slope of the relations between *Trait interoceptive accuracy* and *Perceived emotional intensity* was not significantly different from 0 for any level of *Emotion category* (see Table S7 in the Supplemental Materials). Furthermore, we observed both a significant effect of the predictor *Interoceptive sensibility*, $F(1,93) = 4.01$ $p = .048$, as well as a significant interaction between *Emotion category* and *Interoceptive sensibility*, $F(4,4786) = 3.28$, $p = .011$, in predicting *Perceived emotional intensity*. The slope comparisons by *Emotion category* revealed that both neutral and sad expressions were perceived as more emotionally intense with higher *Interoceptive sensibility*: The slope for sad expressions was 0.14, 95% CL [0.00, 0.27], $t(145) = 2.65$, $p = .036$, and the slope for neutral expressions was 0.14, 95% CL [0.01, 0.28], $t(145) = 2.81$, $p = .027$ (see Figure 5A). Similar to the main analysis, excluding *Alexithymia* did not change the outcomes in a meaningful way. The complete model fits, including effects that are unrelated to our predictors of interest, can be found in Tables S6 and S8 in the Supplemental Materials.

In the Bayesian LMM with *Confidence in emotion recognition* as outcome, estimated slopes at three points of the *Autistic traits* distribution were not robustly different from zero across and within the emotional expression categories (see Table S9 in the Supplemental Materials for all slope comparisons). This suggests that *Confidence in emotion recognition* might not be affected by autistic trait levels.

The same was the case for *Interoceptive sensibility*. For neutral expressions, we did, however, find robust evidence for a positive estimated slope at average *Trait interoceptive accuracy*, slope = 0.03, 95% HPD [0.00, 0.06], and "high" (mean + 1SD) *Trait interoceptive accuracy*, slope = 0.03, 95% HPD [0.00, 0.06], with both Highest Posterior Density (HPD) intervals excluding zero. Thus, specifically when evaluating neutral expressions, individuals with a higher *Trait interoceptive accuracy* were more confident in their decisions (see Figure 4E).

Discussion

As expected, we found evidence for a reduced emotion recognition performance with higher autistic trait levels. Yet, only angry facial expressions were significantly less recognized in our experiment. Furthermore, against our hypotheses, higher autistic traits were not associated with a lower trait interoceptive accuracy, both when and when not controlling for alexithymia. Trait interoceptive accuracy was also neither directly linked to emotion recognition accuracy nor had an indirect effect in the association between autistic traits and recognition of angry expressions. The exploratory analyses, however, showed that individuals with higher trait interoceptive accuracy were more confident in judging neutral expressions, and that both neutral and sad expressions were perceived as more emotionally intense with higher interoceptive sensibility. Autistic traits, in contrast, were neither associated with alterations in confidence judgment nor in perceived intensity of emotional expressions.

Taken together, trait interoceptive accuracy did not play a role in altered emotion recognition with higher autistic trait levels, and was not even directly related to emotion recognition outcomes. Yet, interoception might still have an influence on emotion processing as interoceptive sensibility, that is the subjective awareness of bodily signals, affected the perceived intensity of some facial expressions, and trait interoceptive accuracy was linked to confidence ratings associated with recognizing neutral expressions. Being performed in an online setting, we had no insights in an individual's objective interoceptive accuracy as well as their physiological responses to the facial emotional expressions in Experiment 1. These limitations were addressed in Experiment 2 (see Figure 1).

Experiment 2

Method

Participants

For the replication and extension of Experiment 1, we aimed to have a comparable sample to Experiment 1 (see above for rationale). Thus, 105 participants were recruited, either via the online recruitment platform SONA of Leiden university (97 participants) or via in-person advertisement at Leiden university between 04/01/2022 and 02/05/2023. Of this sample, two participants had to be excluded due to diagnosed neurodevelopmental conditions, two participants because of software failure and one participant because of missing data. Our final sample consisted of 100 participants (88 female, 12 male), aged between 18 and 26 years (M = 20.02, SD = 2.11). The majority of our participants were Dutch (57 individuals), then German (11 individuals) and Polish (7 individuals), and all participants completed the experiment in English. There was no monetary reimbursement for participation but Leiden university students could receive 3 course credits. Informed consent was provided prior to participation and the study protocol was approval by the local ethics committee of the Faculty of Social and Behavioural Sciences at Leiden University (2022-03-11-M.E.Kret-V2-3838). The experiment was conducted according to the Declaration of Helsinki.

Stimuli

We used the same stimuli as in Experiment 1.

Procedure

The procedure of the lab study was closely matched to the procedure of the online study (see Figure 1). Participants were brought to a quiet experiment room where the facial electromyography (fEMG) recordings were prepared (see Measurements section). All tasks and questionnaires were presented on a Philips screen with a resolution of 1920 x 1080 pixels (23.6”) which was at approximately 50cm distance of the participant. The background colour of all tasks was uniform grey. Participants always completed an emotion recognition task first (using EPrime 3.0), which was followed by a heartbeat discrimination task (Whitehead et al., 1977; using PsychoPy 2021.2.3) and all questionnaires in an online survey (using Qualtrics, see Measurements section). This fixed task order was chosen to avoid biases in the lab study which might not have been present in the online study or might influence task responses. More specifically, the heartbeat discrimination task was always the second task to avoid priming participants to listen to their body signals while performing the emotion recognition task. We also did not want participants to be biased in their responses in the heartbeat discrimination task by activating beliefs about general interoceptive abilities via the questionnaires. Therefore, the questionnaires were always completed last. Experimenters were always present in the room during the instruction and practice phases of each task, and left the room for the main task as well as for the questionnaires.

The trial structure of the emotion recognition task in the lab study was the same as in the online study: After a central fixation cross lasting 1s, a randomly selected facial expressions video (see Stimuli section) was presented in the centre of the screen for 2s (720 x 480 pixels, average visual angle: 22.12° horizontal and 14.85° vertical). A 100ms blank screen was then followed by a screen with questions on the emotion label, on confidence in the emotion label decision and on the perceived emotional intensity of the expression (see Procedure section of Study 1). Upon completion of the emotion recognition task, the fEMG electrodes were removed from the participants' faces, and three electrodes for the electrocardiogram (ECG) were applied to the participants' upper bodies (see Supplemental Materials). To perform the heartbeat discrimination task (Whitehead et al., 1977), participants were given the instruction to judge whether a set of five tones is played "in sync" or "out of sync" with their own heartbeats via key press. Auditory feedback on R-peaks with a delay of 200ms is typically perceived as synchronously by participants with a high cardiac interoceptive accuracy, and a delay of 500ms is perceived as delayed (Ring & Brener, 2018). The usage of multiple delays can provide a better and more individualized estimate of a participant's cardiac interoceptive accuracy (method of constant stimuli (Kleckner et al., 2015)). When piloting the task used in the current study, colleagues found that the interoceptive accuracy index resulting from the two interval method was more closely linked to other measures of interoception than the interoceptive accuracy index from the method of constant stimuli, while the two measures were correlated. As it also requires less time to complete, we decided to use the two interval method for the current study. After a 2min baseline heart rate recording, \ participants judged the synchronicity of five black dots appearing simultaneously (or delayed) with five tones as a practice (four trials). Each trial of the heartbeat discrimination task started with the visual presentation of numbers counting down from 3 for 3s and a short break (depending on the delay condition), after which participants were presented the five tones via headphones and no visual input (blank grey screen). Once all five tones were played, a question screen appeared asking the participants to judge whether the tones were "in sync" or "out of sync" with their heartbeats by key press. On a second screen, they had to indicate the confidence in their decision on a visual analogue scale from "total guess/no heartbeat awareness" to "complete confidence/full perception of heartbeat". Integer values ranged from 0-100 but were not visible to the participant. All judgments were made in a self-paced manner. Participants completed 60 trials of the heartbeat discrimination task in total (30 per delay condition). Once the task was completed, the ECG electrodes were removed from the participants' bodies, and they filled in the questionnaires (see Measurements section) in a randomized order after providing demographical information regarding their age, gender, and nationality.

Measurements

Facial electromyography (fEMG). We used facial electromyography (fEMG) as technique to derive mimicry of the presented emotional expressions. Following the guidelines of Fridlund and Cacioppo (1986), we placed a reusable 4 mm Ag/AgCl surface electrode as a ground electrode on the top of the participants' foreheads, two electrodes of the same type over the Corrugator Supercilii region (referred to as "corrugator" hereafter) above the participants' left eyebrows, and two electrodes over the Zygomaticus Major region (referred to as "zygomaticus" hereafter), that is on the participants' left cheeks. Expressions of sadness, fear and anger are typically associated with increased activations of the corrugator whereas happiness expressions are associated with a decreased activation (i.e., a relaxation) compared to neutral expressions (e.g., Folz et al., 2022; Künecke et al., 2014). Additionally, increased activation over the zygomaticus region typically occurs when happiness is expressed. Thus, facial mimicry of the presented expressions should result in similar muscle activations. The fEMG signal was recorded at a sampling rate of 1000 Hz, using a Biopac MP150 system (see Supplemental Materials for details on the data recording and preprocessing). For each trial, separate epochs were defined for the first 500ms of each video with a neutral expression (as baseline) and the 1.5s in which the emotional expression was shown (as response). Based on an automated detection of extreme values as well as manual coding, 41 trials of the preprocessed corrugator data (1%) and 149 trials of the preprocessed zygomaticus data (3%) were excluded from further processing. Data of each trial was baseline-corrected by subtraction, z-scored by participant and muscle region and averaged within the response window of each trial.

Electrocardiography. We recorded the participants' electrocardiograms to provide (delayed) auditory feedback about heartbeats in the heartbeat discrimination task (see Procedure section). Three disposable 35mm AG/AgCl electrodes were attached to the participants' upper bodies. The negative electrode (Vin-) was placed under the right collarbone, the positive electrode (Vin+) on the left bottom rib, and the ground electrode below the right ribs. The data was recorded with a sampling rate of 1000Hz using a BIOPAC MP150 system (see Supplemental Materials for details on data recording and preprocessing). As irregularities in the ECG recordings might have resulted in imprecise heartbeat feedback, we visually inspected the recorded data and excluded trials with irregularities from calculating objective interoception measures.

Cardiac interoceptive accuracy and interoceptive trait prediction error. We calculated cardiac interoceptive accuracy by dividing the number of trials that were correctly responded to in the heartbeat discrimination task by the total number of trials (excluding trials with irregularities). To rule out that differences in baseline heart rate could explain individual differences in cardiac interoceptive accuracy, we calculated a correlation (Spearman's rank) between the two measures, which was not significant ($p = 0.69$). The interoceptive trait prediction error was calculated according to Garfinkel et al. (2016): Both cardiac interoceptive accuracy scores and interoceptive sensibility scores were centered and scaled. Then, the difference between the two values was calculated for each participant as a measure of their individual interoception trait prediction error, with positive scores reflecting an overestimation and negative scores reflecting an underestimation of interoceptive abilities. Information about the distribution of both interoception measure scores can be found in Table 3.

Interoceptive attention. We used the Interoceptive Attention Scale (IATS; Gabriele et al., 2022) to assess self-reported interoceptive attention regarding a variety of body sensations (e.g., heartbeat, hunger, need to urinate,..). Interoceptive attention for each of the 21 IATS-items are rated on a 5-point Likert scale (1 = disagree strongly, 2 = disagree, 3 = neither agree nor disagree, 4 = agree, and 5 = strongly agree). Descriptive information about all questionnaires scores in Experiment 2, including an overview of the questionnaire reliabilities and distribution parameter, can be found in Table 3. A visualization of the relations between the questionnaire measures, as well as the measures from the heartbeat discrimination task, can be found in Figure S1B in the Supplemental Materials.

Interoceptive sensibility. While the same 26 items as in Experiment 1 were used to calculate interoceptive sensibility (i.e., the items of BPQ-SF body awareness scale, see Table 3), participants additionally completed the 20 other items of the BPQ full version body awareness scale in Experiment 2. In addition, we asked the same control question as for the Interoceptive Attention Scale (Gabriele et al., 2022) to unveil whether participants interpreted this scale as a measure of interoceptive accuracy, interoceptive attention or actual frequency and/or intensity of body sensations.

Autistic traits, Social anxiety traits, Alexithymia. To assess autistic traits, social anxiety traits and alexithymia, the same questionnaires were used as in Experiment 1. Descriptive statistics and information about the distribution and reliability are summarized in Table 3.

Table 3. Distribution of questionnaires scores, including their internal consistency (Cronbach's Alpha) and distribution parameters, as well as objective interoceptive accuracy measures in the lab study (Experiment 2)

	N	Mean	SD	Min	Max	α	lCL	hCL	kurtosis	skewness
AQ	100	17.30	5.82	4	38	0.72	0.64	0.80	3.69	0.32
IAS	100	75.64	8.59	53	98	0.74	0.67	0.81	3.21	0.09
BPQ	100	74.16	17.14	39	112	0.91	0.88	0.93	2.24	-0.07
LSAS	100	48.73	20.52	0	120	0.93	0.91	0.95	3.65	0.27
TAS	100	48.25	11.64	24	77	0.84	0.79	0.88	2.60	0.19
IATS	100	57.22	12.54	21	87	0.88	0.84	0.91	2.88	0.09
Cardiac IA	100	0.54	0.08	0.33	0.85				5.31	0.64
ITPE	100	0.00	1.41	-4.94	3.33				3.82	-0.52

Note. AQ = Autism Quotient (Autistic traits), IAS = Interoceptive Accuracy Scale (Trait interoceptive accuracy), BPQ = Body Perception Questionnaire (Interoceptive sensibility), LSAS = Liebowitz Social Anxiety Scale (Social anxiety traits), TAS = Toronto Alexithymia Scale (Alexithymia), IATS = Interoceptive Attention Scale (Trait interoceptive attention), Cardiac IA = Cardiac interoceptive accuracy, ITPE = Interoceptive trait prediction error, lCL/hCL = lower/higher Confidence Level of 95% Confidence Interval associated with α.

Data Analysis

All analyses were preregistered on OSF (https://osf.io/97a6e). As explained in the Data Analysis section of Experiment 1, we focused on *Autistic traits* as main predictor in our analyses. Comparable to Experiment 1, significant medium positive correlations between *Autistic traits*, *Social anxiety traits* and *Alexithymia* were observed (LSAS-AQ: $r_s = 0.32$, $p = .001$; LSAS-TAS: $r_s = 0.25$, $p = .01$; AQ-TAS: $r_s = 0.35$, $p < .001$). Prior to model fitting, all continuous variables were standardized (i.e., centered and scaled) to obtain standardized beta coefficients. As a first step, we replicated the mediation analysis as outlined in the Data analysis section of Experiment 1 by fitting three models, using the lmerTest package (Kuznetsova et al., 2017), and quantifying the indirect effect of *Trait interoceptive accuracy* in the association between *Autisitc traits* and *Emotion recognition accuracy* for specific *Emotion category* levels using the RMediation package (Tofighi, 2023). We also explored once again whether *Autistic traits*, *Trait interoceptive accuracy* or *Interoceptive sensibility* would be systematically linked to variations in (1) *Perceived emotional intensity* and (2) *Confidence in emotion recognition* in two separate models (see Data analysis section of Experiment 1).

As a second step, we investigated how *Cardiac interoceptive accuracy* would relate to subjective measures of interoception (*Trait interoceptive accuracy* and *Trait interoceptive attention*) and *Autistic traits* by running two zero-order correlation analyses. According to the 2x2 factor model by Murphy and colleagues (2019), we should observe a significant positive relationship between *Trait interoceptive accuracy* and *Cardiac interoceptive accuracy*, whereas there should be no such relationship between *Trait interoceptive attention* and *Cardiac interoceptive accuracy* . Furthermore, a partial correlation between *Autistic traits* and *Cardiac interoceptive accuracy*, while controlling for *Alexithymia*, was performed. Lastly, a potentially stronger *Interoceptive trait prediction error* with higher *Autistic traits* was examined (Garfinkel et al., 2016), using a zero-order correlation. P-values of the four correlations were adjusted with the Holm-method. To test the expected positive relation between *Cardiac interoceptive accuracy* and *Emotion recognition accuracy*, we fitted a binomial GLMM on *Emotion recognition accuracy* (1= correct, 0 = incorrect) with *Emotion category* (angry, happy, fearful, sad and neutral), *Cardiac interoceptive accuracy* and their interaction as fixed effects, and random intercepts for each participant and each stimulus.

As a third step, we explored whether, with higher autistic trait levels, facial muscle activity would be less predictive of emotion recognition performance for some emotions. To reduce the number of analysis, we decided not to run separate models for each emotion category but to run one model integrating all categories as well as the two muscle regions. More specifically, we fitted a GLMM on *Emotion recognition accuracy* with a three-way interaction between *Emotion category* (angry, happy, fearful, sad and neutral), *Autistic traits* and baseline-corrected, z-scored *Corrugator activity*, a three-way interaction between *Emotion category*, *Autistic traits* and baseline-corrected, z-scored *Zygomaticus activity*, and a two-way interaction between *Emotion category* and *Social anxiety traits*, and *Alexithymia* as control predictors. As in all models, random intercepts for each participant and each stimulus were included.

Results

Replication: Main Analysis Experiment 1

As in Experiment 1, we did not observe a mediation of the effect of *Autistic traits* on *Emotion recognition accuracy* via *Trait interoceptive accuracy* (see Figure 3). The comparison against zero of slopes between *Autistic traits* and *Emotion recognition accuracy* of specific emotions in the first model revealed that only recognition of sad expressions was worse with higher *Autistic traits*, slope = -0.28, 95% CI [-0.54, -0.03], z = -2.86, p = .017 (**path c**, see Figure 4B, as well as Table S13 in the Supplemental Materials for the full model fit). Therefore, an indirect effect of *Trait interoceptive accuracy* on the association between *Autistic traits* and *Emotion recognition accuracy* of exclusively sad expressions was examined (**path ab**). As confidence limits included zero, μ = 0.01, 95% CL[-0.03, 0.06], we again found no indication that trait interoceptive accuracy would mediate worse emotion recognition with higher autistic trait levels.

Next to a robust negative slope for sad expressions, we also observed a robust positive slope in the relation between autistic trait levels and the recognition of neutral expressions, trend = 0.35, 95% CI [0.08, 0.62], z = 3.29, p = .005. Unexpectedly, this observation indicates a better recognition of neutral expressions with higher autistic trait levels (see Figure 4B and Table S13 in the Supplemental Materials). In line with Experiment 1, the predictor *Autistic traits* was not significantly linked to *Trait interoceptive accuracy* in our second model (**path a,** see Table S16 in the Supplemental Materials), and neither *Trait interoceptive accuracy* nor its interaction with *Emotion category* were significant predictors of *Emotion recognition accuracy* (**path b,** see Table S18 in the Supplemental Materials). Again, there was no meaningful change in outcomes if the control predictor *Alexithymia* was excluded from all models with *Autistic traits* as. The model fits of the mediation analysis, including (significant) effects that are unrelated to our predictors of interest, can be found in Tables S13-18 in the Supplemental Materials.

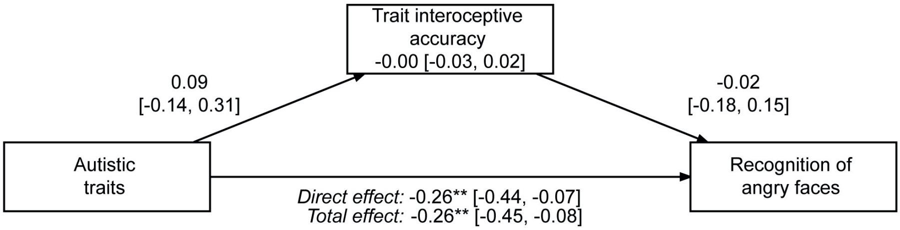
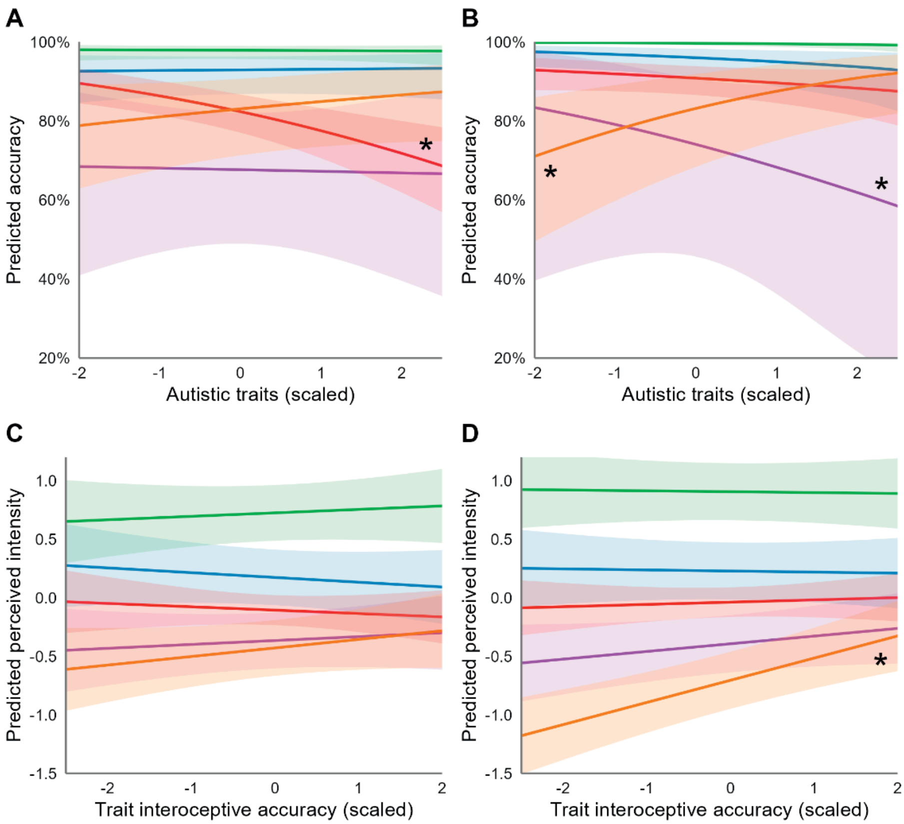


Figure 3. Results of the mediation analysis in Experiment 2 with trait interoceptive accuracy as potential mediator explaining worse recognition of sad faces with higher autistic trait levels. While the coefficient for sad facial expressions in the significant interaction between Autistic traits and Emotion category was not significant, the slope of this effect was robustly negative, which is why we tested for a mediated effect (in line with the main analysis in Experiment 1).



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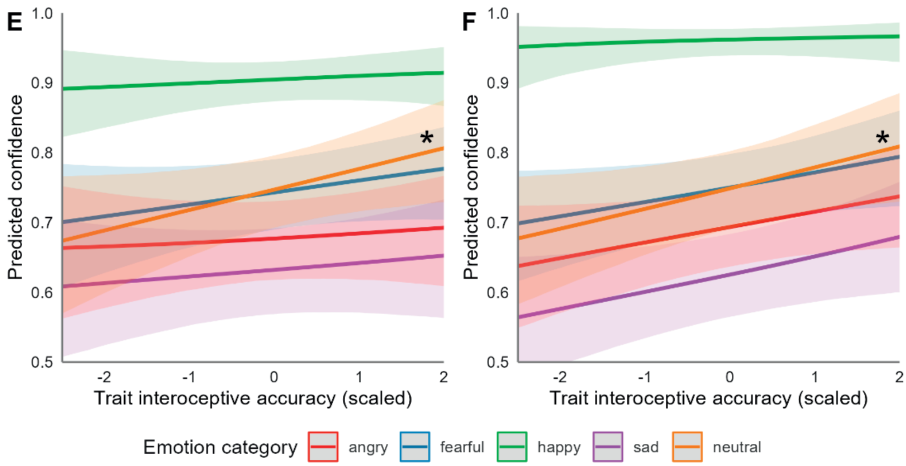

Figure 4. Replicated significant interactions between self-report measures and categories of facial expressions in predicting emotion recognition task outcomes (Experiment 1 on the left and Experiment 2 on the right). Asterisks indicate robust negative/positive slopes for specific emotion categories in the slope comparison against zero. Shaded areas represent 95% confidence boundaries. Predicted accuracy and predicted confidence are on a scale from 0-1, while perceived emotional intensity is centred and scaled, with 0 representing the mean and 1 representing the value at 1 SD.

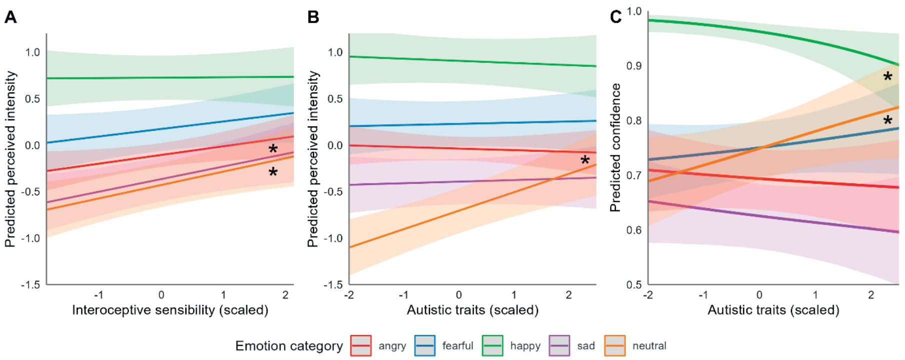

Figure 5. Non-replicated significant interactions between self-report measures and categories of facial expressions in predicting emotion recognition task outcomes in Experiment 1 (A) and Experiment 2 (B+C). Asterisks indicate robust negative/positive slopes for specific emotion categories in the slope comparison against zero. Shaded areas represent 95% confidence boundaries. Predicted accuracy and predicted confidence are on a scale from 0-1, while perceived emotional intensity is centred and scaled, with 0 representing the mean and 1 representing the value at 1 SD.

Replication: Exploratory Analyses Experiment 1

As in Experiment 1, we observed a significant interaction between *Trait interoceptive accuracy* and *Emotion category*, $F(1,4835) = 14.28$, $p < .001$, in the model with *Perceived emotional intensity* as an outcome (see Figure 4D and Table S19 in the

Supplemental Materials for the full model fit). While the linear relations between *Trait interoceptive accuracy* and *Perceived emotional intensity* varied between emotion categories, the slope of the relation was only significantly different from 0 for neutral expressions (see Table 4 for all slope comparisons of significant interactions). In addition, the interaction between *Emotion category* and *Autistic traits* was significant, $F(1,4835) = 17.26$, $p < .001$ (see Figure 5B). We again observed variation between emotion categories regarding the relation between *Autistic traits* and *Perceived emotional intensity* (see Table S19 in the Supplemental Materials for the coefficients). Neutral expressions were, however, again the only emotion category for which the slope was significantly different from zero (see Table 4). As opposed to Experiment 1, the interaction between *Interoceptive sensibility* and *Emotion category* was not significant in this model (similar results for the model without *Alexithymia* can be found in Table S20 in the Supplemental Materials).

Table 4. Estimated slope of the linear relation between self-report measures and perceived emotional intensity by emotion category, and results of the slope comparisons against zero

Self-report measure		Estimated slope	95% CI	df	t-ratio	p-value
Interoceptive accuracy (IAS)	*Emotion category*					
	Angry	0.02	-0.10, 0.14	144	0.43	1
	Fearful	-0.01	-0.13, 0.11	144	-0.21	1
	Happy	-0.01	-0.12, 0.11	144	-0.17	1
	Sad	0.07	-0.05, 0.18	144	1.47	0.58
	Neutral	0.19	0.07, 0.31	144	4.23	**< .001**
Autistic traits (AQ)	*Emotion category*					
	Angry	-0.02	-0.14, 0.10	140	-0.37	1
	Fearful	0.01	-0.11, 0.13	140	0.28	1
	Happy	-0.02	-0.14, 0.10	140	-0.50	1
	Sad	0.02	-0.10 0.14	140	0.37	1
	Neutral	0.20	0.00, 0.32	140	4.29	**< .001**

Note. Confidence intervals are adjusted for multiple comparisons using the Bonferroni-method, and p-values are adjusted using the Holm-method.

In contrast to Experiment 1, estimated slopes at all three examined points of the *Autistic traits* distribution (mean – 1SD, mean, mean + 1SD) were negative and robustly different from zero for happy facial expressions in the Bayesian LMM with *Confidence in emotion recognition* as outcome (see Table 5). This indicates that, across wide parts of the distribution, there was a significant trend for lower confidence in the recognition of happy expressions with higher *Autistic traits* (see Figure 5C). Moreover, for neutral expressions, we found robust evidence for a positive estimated slope at average *Autistic traits* (see Table 5). Thus, especially at average and "high" autistic trait levels, confidence in the recognition of neutral expressions seems to increase with higher trait levels, matching the findings regarding a better recognition of neutral expressions with higher trait levels. We also observed a significant positive slope at all three examined points of the *Trait interoceptive accuracy* distribution (mean – 1SD, mean, mean + 1SD) across emotions. When splitting by emotional expression categories, the robust positive slope only remained significant for neutral expressions at "low"(mean – 1SD) and average *Trait interoceptive accuracy* (see Table 5). Thus, the effect of higher confidence in emotion recognition with higher trait interoceptive accuracy seems most pronounced in the evaluation of neutral expressions (see Figure 4F). For all other predictors, slopes were not significantly different from 0 across and within emotion categories.

Table 5. Integrated posterior estimates of the Generalized Linear Mixed Model with a zero-one-inflated family for the slopes of the relation between confidence in emotion recognition and self-report measures at three different values (mean -1SD, mean, mean +1SD)

Self-report measure		**Mean – 1SD Estimated slope [95% HPD]**	**Mean Estimated slope [95% HPD]**	**Mean + 1SD Estimated slope [95% HPD]**
Autistic traits (AQ)		0.00 [-0.02, 0.02]	0.00 [-0.02, 0.02]	0.00 [-0.02, 0.02]
	Emotion category			
	Angry	-0.01 [-0.03, 0.02]	-0.01 [-0.03, 0.02]	-0.01 [-0.03, 0.02]
	Fearful	0.01 [-0.01, 0.03]	0.01 [-0.01, 0.04]	0.01 [-0.01, 0.04]
	Happy	**-0.01 [-0.02, -0.00]**	**-0.02 [-0.03, -0.00]**	**-0.02 [-0.05, -0.00]**
	Sad	-0.01 [-0.04, 0.01]	-0.01 [-0.04, 0.01]	-0.01 [-0.04, 0.02]
	Neutral	0.03 [-0.00, 0.06]	**0.03 [0.00, 0.06]**	**0.03 [0.00, 0.06]**
Interoceptive accuracy (IAS)		**0.02 [0.00, 0.04]**	**0.02 [0.00, 0.04]**	**0.02 [0.00, 0.04]**
	Emotion category			
	Angry	0.02 [-0.00, 0.04]	0.02 [-0.00, 0.05]	0.02 [-0.00, 0.05]
	Fearful	0.02 [-0.02, 0.04]	0.02 [-0.02, 0.05]	0.02 [-0.02, 0.05]
	Happy	0.00 [-0.01, 0.03]	0.00 [-0.01, 0.02]	0.00 [-0.01, 0.01]
	Sad	0.02 [-0.00, 0.04]	0.03 [-0.00, 0.05]	0.03 [-0.00, 0.06]
	Neutral	**0.03 [0.00, 0.06]**	**0.03 [0.00, 0.06]**	0.03 [-0.00, 0.06]

Note. HPD = Highest Posterior Density interval

Cardiac Interoceptive Accuracy and Self-Report Measures of Interoception, Autistic Traits, and Emotion Recognition Accuracy

Using Mahalanobis distance, we identified and removed bivariate outliers in the relation between *Cardiac interoceptive accuracy* and *Trait interoceptive accuracy* (n = 7), *Trait interoceptive attention* (n = 6) and *Autistic traits* (n = 6), as well as in the relation between the *Interoceptive trait prediction error* and *Autistic traits* (n = 5). In line with the theoretical separation between interoceptive accuracy and attention (Gabriele et al., 2022), we did not find a significant relation between *Cardiac interoceptive accuracy* and *Trait interoceptive attention* in our study (p > .05). Contrasting our expectations, *Cardiac interoceptive accuracy* was neither positively related to *Trait interoceptive accuracy* nor negatively related to *Autistic traits* (both with and without controlling for *Alexithymia*). There was a trend towards a higher interoceptive trait prediction error with higher *Autistic traits* (r = .20, p = .05), which did not survive the correction for the four comparisons ($p_{adjusted}$ = .20). The associated correlation matrix can be found in Table S21 in the Supplemental Materials, and a visualization of the relations between all investigated variables Figure S1B in the Supplemental Materials. Lastly, *Cardiac interoceptive accuracy* was not a significant predictor in the GLMM on *Emotion recognition accuracy* (p > .05 for both the main effect and the interaction; see also Table S22 in the Supplemental Materials). As *Cardiac interoceptive accuracy* was not related to any of our variables of interest, we did not further investigate its role in *Emotion recognition accuracy* (related to facial mimicry).

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Facial Mimicry in Emotion Recognition and its Modulation by Autistic Traits

The model examining whether the link between facial muscle responses and recognition accuracy of distinct facial expressions would be modulated by *Autistic traits* did not reveal any effects beyond those already reported for the first model of the results section (see also Table S23 in the Supplemental Materials). Thus, facial muscle responses were not predictive of *Emotion recognition accuracy*, and there was also no effect of *Autistic traits* on this link.

Exploratory Analysis

Neither interoception measures nor facial muscle activations could explain altered emotion recognition associated with autistic traits in this study, or were themselves significant predictors of recognition accuracy. In line with previous work, trait interoceptive accuracy was significantly linked to the perceived emotional intensity of some expressions. Interoceptive signals might thus rather alter the representation of experienced and/or observed emotional states, than indicate their qualia. Surprisingly, however, both higher interoceptive accuracy as well as higher autistic trait levels were specifically associated with a higher perceived emotional intensity of neutral expressions in Experiment 2. From an embodied perspective, there could be two potential explanations why observed neutral expressions might be perceived as emotional: either physiological feedback which typically indicates (the lack of) emotionality might not be integrated in the representation of an expression or physiological signals unrelated to the observed expression might be misinterpreted. While, based on previous literature (Garfinkel et al., 2016; Quattrocki & Friston, 2014), the first explanation seems more plausible for the results regarding autistic traits, the second might explain higher perceived emotional intensity of neutral expressions with higher trait interoceptive accuracy (Dunn et al., 2010).

To explore this idea further, we fitted one large model in which we examined whether facial muscle activations would be linked more strongly to perceived emotional intensity with (a) higher trait interoceptive accuracy and (b) lower autistic trait levels. More specifically, we extended the model predicting *Perceived emotional intensity* by adding four three-way interactions, all including *Emotion category* as well as either one of the two facial muscle activations (baseline-corrected, z-scored *Corrugator activity* or baseline-corrected, z-scored *Zygomaticus activity*) and either one of two self-report measures (*Autistic traits* or *Trait interoceptive accuracy*). Next to these predictors of interest, the model still included a two-way interaction between *Emotion category* and *Interoceptive Sensibility*, a two-way interaction between *Emotion category* and *Social anxiety traits,* and *Alexithymia* as control predictors. As in all previous models, random intercepts for each stimulus and each participant were added. The results of this extended intensity model indeed suggest that the directionality of the effect of facial muscle activation on intensity ratings might depend on the trait dimension. More specifically, while both *Corrugator activity* and *Zygomaticus activity* seem to be less predictive of *Perceived emotional intensity* across emotions with higher *Autistic traits*, $\beta = -0.03$, 95% CI[-0.06, -0.01] and $\beta = -0.02$, 95% CI [-0.05,-0.00] (see Figure 6A+B), there was a trend of *Zygomaticus activity* being more predictive of *Perceived emotional intensity* with higher *Trait interoceptive accuracy*, $\beta = 0.02$, 95% CI [-0.00,0.05] (see Figure 6C, and Table S24 in the Supplemental Materials for the full model fit).

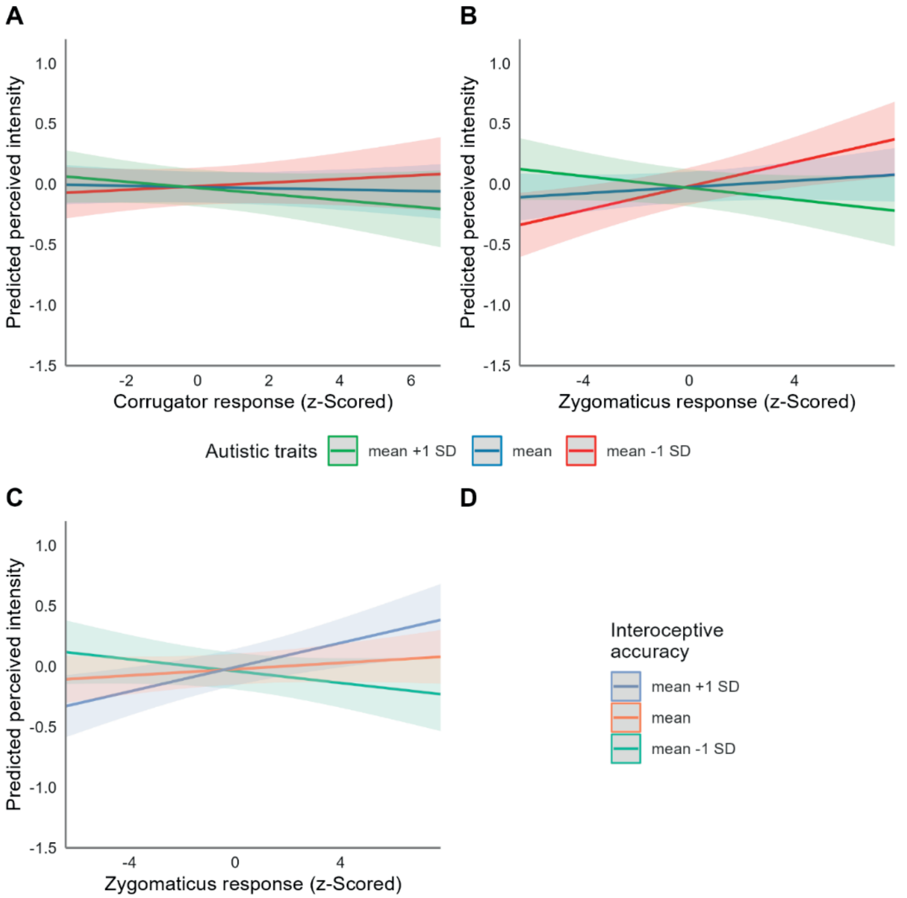

Figure 6. Modulation of the links between facial muscle responses to observed facial expressions and perceived emotional intensity by self-report measures. Continuous self-report measures are split in groups for visualization purposes. Perceived emotional intensity is centered and scaled, with 0 representing the mean and 1 representing the value at 1 SD. Shaded areas represent 95% confidence boundaries.

Sensitivity Analyses

The distributions of both baseline-corrected, averaged and z-scored facial muscle activity signals were highly leptokurtic (kurtosis of 7.65 and 17.83 for corrugator and zygomaticus respectively). To gauge the potential influence of extreme outliers on our findings, we decided to run sensitivity analyses for the models including *Corrugator activity* and *Zygomaticus activity* as predictors. More specifically, we transformed the distribution of the two variables to be as close to Gaussian as possible, using the Gaussianize function of the LambertW R package (Goerg, 2022), and re-ran the last two analyses of this results section. The corresponding model

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fits were in line with our original findings: Facial muscle activity remained not predictive of emotion recognition accuracy, and autistic traits did not modulate the relation between the two. Mirroring the results of the exploratory analysis, both gaussianized *Corrugator activity* and gaussianized *Zygomaticus activity* were less predictive of *Perceived emotional intensity* with higher *Autistic traits*, while, with higher *Trait interoceptive accuracy*, gaussianized *Zygomaticus activity* was more predictive of *Perceived emotional intensity* (see Tables S25 and S26 in the Supplemental Materials). Lastly, we aimed to investigate potential systematic effects of response biases in evaluating emotion recognition accuracy in both experiments. Therefore, we calculated each participant's *Unbiased Hit Rates* (i.e., Hu scores; Wagner, 1993) for each emotion category and predicted those by *Autistic traits,* mirroring the first model fits of the mediator models (see Supplemental Materials for more information). Links between *Autistic traits* and *Unbiased Hit Rates* were similar to the results of the main analysis in Experiment 1, whereas there was no evidence for less accurate recognition of sad facial expression with higher Autistic traits in Experiment 2 when looking at *Unbiased Hit Rates*.

Discussion

In the lab study, we could replicate most of the observations that were made in the online study (Experiment 1): First, we did not find evidence for trait interoceptive accuracy being a mediator in the link between autistic trait levels and emotion recognition accuracy, neither being a direct predictor of recognition accuracy. Surprisingly, while accuracy also showed to be reduced with higher autistic trait levels for a specific emotion, this specific emotion was sadness and not anger (as in Experiment 1). Further, recognition of neutral expressions was even increased with higher autistic trait levels in Experiment 2. In line with Experiment 1, higher trait interoceptive accuracy was also linked to a higher perceived intensity of neutral expressions, as well as more confidence in their recognition. In contrast to Experiment 1, we did not find an effect of interoceptive sensibility on perceived emotional intensity. Instead, we found significant effects of autistic traits on the perceived emotional intensity of neutral expressions, as well as on the confidence in recognizing them. Similarly to the results linked to interoceptive accuracy, neutral expressions were rated higher in emotional intensity and confidence in rating them correctly was increased with higher autistic trait levels. Our exploratory analysis indicated that these seemingly contradicting findings might be the result of integrating actual physiological signals more or less strongly, respectively, in emotional intensity judgments. Confidence in rating happy expressions, in contrast, decreased with higher autistic trait levels. Expanding our models by including objective measures of interoceptive accuracy or physiological changes (i.e., facial muscle responses) in Experiment 2 did not aid to explain emotion recognition accuracy, as well as potential alterations with higher autistic trait levels. Our measure of interoceptive accuracy was also not related to subjective interoceptive accuracy, or any other interoception measure.

General Discussion

Taken the results of our two experiments together, we did not find evidence for either self-reported (trait) or objective (cardiac) interoceptive accuracy explaining modulations in emotion recognition accuracy linked to autistic trait levels. While we did observe lower recognition performance for distinct emotional expressions with higher autistic trait levels, we did not find systematic differences in accuracy linked to individuals' interoceptive abilities. Trait interoceptive accuracy (and interoceptive sensibility in Experiment 1) was rather linked to confidence in emotion recognition as well as the perceived emotional intensity of observed expressions. In contrast to a previous study, facial muscle responses were not predictive of accurately recognizing specific emotional expressions, and the relation between facial muscle responses and emotion recognition accuracy was not altered by an individual's autistic trait levels in the current lab study. Our exploratory analyses, however, indicated that facial muscle activations might be more or less strongly linked to the perceived emotional intensity of an observed expressions, depending on an individuals' trait interoceptive accuracy and autistic trait levels respectively. Thus, as physiological responses and their sensation seem to play a role in altered facial emotion processing in non-autistic individuals with higher autistic trait levels, an examination of their relevance in altered facial emotion processing in autism might yield promising insights.

In line with our expectations, we found some evidence for reduced emotion recognition performance with higher autistic trait levels in our non-autistic sample. Yet, the effect was specific to certain emotion categories and differed between the two experiments (Experiment 1: anger, Experiment 2: sadness). Inconsistent results with regard to the recognition of distinct facial emotional expressions have also been reported in autistic samples, suggesting specifically worse recognition performance of fear (Uljarevic & Hamilton, 2013), sadness (Wallace et al., 2011), disgust (Enticott et al., 2014; Law Smith et al., 2010), happiness (Eack et al., 2015), or anger (Enticott et al., 2014). While differences in task demands, including stimuli and task complexity, have been suggested as one cause of inconsistencies in autistic samples (Harms et al., 2010), this could not have been the case in the current study, as the same emotion recognition task was performed in both experiments. There were, however, systematic differences in the experimental setting and in sample characteristics, which could have driven the diverging results. Moreover, systematic response biases can distort accuracy scores in categorical judgments (Wagner, 1993), such as on observed emotional facial expressions. In our case, additional analyses with unbiased recognition scores as outcome indicated that these distortions might have played a role in the observed reduced recognition of sad expressions with higher autistic trait levels in Experiment 2, but likely not in the observed reduced recognition of angry expressions (Experiment 1) or the observed increased recognition of neutral expressions (Experiment 2) with higher autistic trait levels (see Supplemental Materials).

This increased recognition of neutral facial expressions with higher autistic trait levels in Experiment 2 unexpected. Perceiving emotionality in neutral facial expressions is a commonly made mistake in the general population, and this bias has been associated with the importance of facial emotion perception in navigating our social world (Albohn Daniel N.and Brandenburg, 2019). By following a rule-based path to facial emotion recognition, which rather relies on the presence/absence of distinct features (Rutherford & McIntosh, 2007), one might be less prone to incorrectly interpret emotionality into neutral faces (i.e., less "false alarms"). Individuals on the autism spectrum have been suggested to follow this rule-based path to emotion recognition, as might non-autistic individuals with high autistic trait levels. The interpretation of facial expressions could further be facilitated by an accurate sensation of physiological signal changes in an emotion recognition context. Based on interoception research in autism (DuBois et al., 2016), we assumed that this path to emotion recognition might be less reliable in non-autistic individuals with higher autistic trait levels. Against our expectations, we did not find that interoceptive accuracy predicted emotion recognition accuracy, or mediated the negative relation between autistic trait levels and recognition of specific facial expressions. Facial muscle responses were not less predictive of emotion recognition accuracy with higher autistic trait levels as found in a previous study. While our initial hypotheses were not supported in the current study, the findings, nevertheless, offer further insights into the conceptualisation of interoception, its potential role in facial emotion perception as well as putative interoceptive alterations associated with autistic trait levels within this context.

Contradicting previous findings (Murphy et al., 2020), cardiac interoceptive accuracy, measured via the heartbeat discrimination task, was not associated with trait interoceptive accuracy, measured via the interoceptive accuracy scale, in the current study. The use of classic cardiac interoception tasks to assess interoceptive accuracy has recently been heavily criticized. They are likely to be confounded by the reliance on additional cognitive processes (Hickman et al., 2020; Ring & Brener, 2018) and only focus on one interoceptive domain (i.e., cardioception) as well as few dimensions of interoception, neglecting its multidomain and multidimensional nature (Suksasilp & Garfinkel, 2022). The few previous studies comparing the performance of individuals on the autism spectrum to non-autistic controls in heartbeat discrimination tasks did not find a robustly reduced interoceptive accuracy (Z. J. Williams et al., 2023). We did not find a significant negative relationship between cardiac interoceptive accuracy and autistic trait levels in our non-autistic sample either, and, unexpectedly, also no relations between self-reported measures of interoception (i.e., accuracy and sensibility) and autistic traits. Importantly, the expectations on links between interoception measures and autistic trait levels in our non-autistic sample were based on results of studies with individuals on the autism spectrum, who might differ in their interoceptive processing. Alexithymia, in contrast, showed the expected negative relation to trait interoceptive accuracy. While recent perspectives claim that alexithymia might underlie emotion recognition difficulties in autism, our findings on links between autistic traits and all emotion recognition task outcomes in a non-autistic sample did, not change depending on whether alexithymia was included as control predictor or not. Whether alexithymia does play a role in altered facial emotion recognition with higher autistic trait levels in non-autistic individuals, or whether it might only become relevant in autism is to be further investigated.

Higher interoceptive accuracy has been associated with more flexibility in the precision of interoceptive prediction errors (i.e., the potential to increase precision via attention) in the predictive coding perspective, whereas extremely precise, inflexible priors have been proposed as source of interoceptive difficulties in autism (Quattrocki & Friston, 2014). These alterations in priors might already, to some degree, be present in non-autistic individuals with high autistic trait levels, as other phenomena that are associated with autism Our findings regarding the differential effect of trait interoceptive accuracy and autistic traits on the link between facial muscle activity and perceived emotional intensity could be interpreted as support for these assumptions: In individuals with high interoceptive accuracy, prediction errors associated with interoceptive signals reflecting facial muscle activations during facial expression observation could have been more influential due to a higher precision via attention. As a consequence, they might have reported perceiving stronger emotional experiences (and potentially also showed stronger physiological reactions), which generalized to neutral expressions. Scoring higher on autistic traits, in contrast, might have been associated with less integration of interoceptive information about facial muscle activations on high-level processing, i.e., in attributing emotionality to observed facial expressions. In those lines, higher confidence in the recognition of neutral expressions might be the product of different processes in relation to autistic traits versus trait interoceptive accuracy. With higher autistic traits, recognition of neutral expressions was indeed better, which could relate to a rule-based path to emotion recognition: Not identifying clear indicators of a specific emotion category could have resulted in higher confidence ratings regarding the categorization of neutral expressions, while undefined physiological arousal could have still resulted in rating them as more intense. Lower confidence in recognizing happy expressions, in contrast, might result from integrating mimicry responses less, which are usually most pronounced for happy facial expressions. General higher confidence ratings with higher trait interoceptive accuracy, and specifically for neutral expressions, could be a result of more strongly perceived physiological feedback which reinforced confidence in all labelling decisions (similar to perceived emotional intensity). These are, however, only assumptions which should be tested more systematically in future studies.

Both autistic trait levels as well as interoceptive accuracy modulated the link between instant facial muscle activations and perceived emotional intensity of expressions. This indicates that the integration of one's own physiological feedback in processing other's emotions seems to differ between individuals, and specifically seems to be reduced with higher autistic trait levels in the general population. Training one's interoceptive abilities might thus be useful to gain emotional clarity not only about one's own but also about others' emotions. The effect of enhancing interoceptive processing with different interventions has already been investigated with varying complexity and on multiple time scales. Priming an interoceptive focus in the general population, for example, has been shown to improve emotion recognition when using a heartbeat counting task (Salamone et al., 2021), but not when using instructions (Bornemann et al., 2012). Addressing interoceptive processing more broadly and on a longer time-scale, (brief) mindfulness interventions have been shown to have a small but significant effect in reducing negative affect in non-clinical and clinically diverse samples (Schumer et al., 2018). For example, online mindfulness interventions have been found to be similarly successful as online cognitive behaviour therapy in reducing anxiety symptoms in some individuals on the autism spectrum (Gaigg et al., 2020). The novel Aligning Dimensions of Interoceptive Experience (ADIE) therapy, which specially focusses on addressing the mismatch between cardiac interoceptive sensibility and accuracy (Quadt et al., 2021), confirms the potential of interoception-based interventions to alleviate anxiety in individuals on the autism spectrum. While the effectiveness of interventions targeting interoception has mainly been investigated in relation to anxiety in autism, interoception also plays a fundamental role in representing the self versus the other (Gao et al., 2019; Palmer & Tsakiris, 2018), including emotional states (Engelen et al., 2023). Given that altered self-other distinction has been linked to social difficulties in autism (Lamm et al., 2016; Lombardo et al., 2010), the usefulness of interoception interventions in strengthening self-other knowledge, including the affective domain, should be examined in future research.

The main objective of our study was to get a better understanding of the role of interoception and physiological responses (i.e., facial mimicry) in emotion processing in relation to autistic trait levels. By closely matching the lab study (Experiment 2) to the preceding online study (Experiment 1), we successfully unveiled robust modulations in the associations between some self-report measures and emotion recognition outcomes. Yet, not all findings could be replicated in the lab study, and some novel observations were made. This could be explained by differences in the experimental setting and the addition of measures (i.e., questionnaires, physiological recordings and tasks). Furthermore, the sample in Experiment 1 was likely more varied in terms of education and lifestyle than the sample in Experiment 2. Thirty percent of the participants in Experiment 1 were not directly recruited at Leiden university whereas we exclusively recruited at Leiden university for Experiment 2. Participants in both experiments were, nevertheless, majorly female young adults, which limits the generalizability of our results. Age and gender differences have been reported with regard to emotion perception and interoception measures (Grabauskaitė et al., 2017), next to gender differences in autistic traits (Ruzich et al., 2015). Future experiments should therefore not only examine whether our findings could be extended to a clinical population (i.e., individuals with an autism spectrum diagnosis), but also more diverse non-autistic samples. While limitations of the heartbeat discrimination task have already been addressed earlier, computerized emotion recognition tasks can never fully reflect emotion recognition in a naturalistic context. By adding task demands to the perception of facial expressions, spontaneous reactions might be altered and processing of expressions might be biased. An experimental context, which requires labelling of facial expressions and already provides categories for it, might activate a top-down mode and reinforce a specific path to emotion recognition, such as visual matching with mental representations (Keating & Cook, 2023). Bodily responses might thus not act as simulations of specific emotional states but rather reinforce perceived emotionality and confidence in one's decisions in people with higher self-reported interoceptive abilities. Whether interoception could become a relevant factor in emotion recognition in daily life, and whether the path to emotion recognition involving interoception is less commonly used in individuals with higher autistic trait levels (or on the autism spectrum), still needs to be further investigated with more ecologically valid and naturalistic paradigms.

Many different paths can lead to recognizing another person's emotion based on their facial expression. Feedback from our own bodies might be one of them, which might be less strongly pronounced in autism. In the current study, we did not find support for reduced interoceptive accuracy explaining worse emotion recognition performance with higher autistic trait levels. Nevertheless, higher trait interoceptive accuracy (and sensibility) resulted in more confidence in labelling expressions as well as in higher perceived emotional intensity ratings of expressions with little or no visual indication of emotionality. Based on the outcomes of an exploratory analysis, we suggest that this might be associated with a stronger integration of actual physiological signals indicating an emotional experience. Higher autistic trait levels, in contrast, might be associated with less integration of physiological signals in determining the emotional intensity of an observed expression. These suggestions should be carefully tested in future studies. With more and more research highlighting the role of interoception in experiencing emotions and connecting to others, fostering adaptive interoceptive processing might become an important avenue in facilitating everyday life social encounters in individuals on the autism spectrum.

Chapter 6

The Role of the Body in Altered Facial Emotion Perception in Autism and Social Anxiety

Abstract

Alterations in the perception of facial emotional expression and their physiological resonance, as well as in accurately sensing bodily states (i.e., interoception) have been reported in both autism and social anxiety. In the current study, we aimed to examine the association between physiological responses, their sensation, and facial emotion perception in individuals on the autism spectrum (N = 40), individuals with social anxiety (N = 27) and neurotypical controls (N = 40). Participants first viewed videos of spontaneous facial expressions (anger, happiness, sadness, fear and neutral) while facial muscle responses (corrugator supercilii and zygomaticus major), indicating facial mimicry, and skin conductance, indicating emotional arousal, were recorded. In a separate task, the same expressions were judged regarding their emotion category, the confidence in the accuracy of this judgment, and the intensity of the observed emotional experience. Compared to controls, individuals with social anxiety showed a stronger link between physiological arousal and the perceived intensity of sadness. Individuals on the autism spectrum showed a relatively weaker link between the mimicry of anger and the intensity at which this expression was perceived. Differences in self-reported interoceptive accuracy also played a role in the latter link, suggesting alterations in integrating embodied emotions in autism.

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Data availability statement:
The datasets and materials generated and/or analysed during the current study will be made available on Dataverse NL upon publication: https://doi.org/10.34894/LUZANN

Supplementary material:

The expression "I feel you" does not exist without a reason: embodied perspectives on social cognition highlight our bodies as platforms to co-represent perceived bodily states of others, thereby gaining information about their mental states, including emotional experiences (Niedenthal, 2007). Yet, individuals differ in their bodily responses to others' emotions (Fawcett et al., 2022) as well as in the sensation of their internal states (i.e., interoception; Murphy et al., 2020), which might, in turn, influence how emotions of others are processed (Terasawa et al., 2014). Distinct alterations in facial emotion perception as well as in physiological reactivity to others' emotions have been reported in individuals on the autism spectrum and individuals with social anxiety (Gilboa-Schechtman & Shachar-Lavie, 2013; Hubert et al., 2009; Uljarevic & Hamilton, 2013; Vrana & Gross, 2004), contributing to social interaction difficulties. Yet, these processes have mainly been investigated separately, and little is known about potential alterations in the direct integration of physiological feedback in processing others' emotions in autism and social anxiety[4]. The current study aims to unveil condition-specific alterations in the links between physiological changes in response to facial emotional expressions and facial emotion perception, and to explore the role of individuals' differences in interoception therewithin.

Facial Emotion Perception Alterations in Autism and Social Anxiety Disorder

Facial emotion perception in autism has been extensively researched, and most studies show lower accuracies in the recognition of all facial expressions of basic emotions (Uljarevic & Hamilton, 2013; Yeung, 2022). While results have long been interpreted as evidence for "deficits" in emotion processing, recent approaches highlight the different paths to emotion recognition that individuals on the autism spectrum would employ (Keating et al., 2023; Rutherford & McIntosh, 2007). The few studies that investigated the perception of emotional arousal in others' facial expressions in autism have mainly observed that individuals on the autism spectrum report on lower arousal in others' facial emotional expressions compared to neurotypical controls (Schneider et al., 2020; Tseng et al., 2014). Whether individuals on the autism spectrum also show altered confidence in their facial emotion recognition skills is, to date, unclear. Two studies have found no differences between individuals on the autism spectrum and neurotypical controls in how confident they are in their emotion recognition skills (Sawyer et

4 In this manuscript, we aim to adhere to the basic principles of inclusive language by avoiding the term "disorder" and by referring to the clinical conditions as "autism" and "social anxiety". On an individual level, we employ the most widely accepted terminology in the autism community (Botha et al., 2023), using the person-first term "individuals on the autism spectrum" and, accordingly, "individuals with social anxiety".

al., 2014; S. Wang & Adolphs, 2017). In contrast, under- and overestimations of facial emotion recognition accuracy have been associated with higher autistic trait levels in a neurotypical sample (Folz et al., 2023), in line with a similar pattern concerning social skill judgments in a clinical sample (DeBrabander et al., 2020). Hence, modulations in both intensity of perceived facial expressions and confidence in their recognition may also be accounted for by a different path to emotion recognition compared to neurotypical individuals.

Alterations in facial emotion processing have also been observed in social anxiety (for reviews, see Gilboa-Schechtman & Shachar-Lavie, 2013; Machado-de-Sousa et al., 2010). Namely, individuals with social anxiety tend to interpret displays of facial emotions more negatively. This could, for example, result in a higher sensitivity to negative expressions (e.g., Gutiérrez-García & Calvo, 2017; Joormann & Gotlib, 2006; however see Bui et al., 2017) and a lower sensitivity to positive expressions (Lacombe et al., 2023). Moreover, higher misattributions of negative affect to neutral expressions have been observed in individuals with social anxiety (Peschard & Philippot, 2017). This misperception of social threat might explain why emotional facial expressions are reported to be more arousing (Kivity & Huppert, 2016). Yet, not all studies report increased threat perception in faces, including higher intensity of arousal ratings, in socially anxious individuals (e.g., Vrana & Gross, 2004). Recent evidence further suggests that not emotion recognition performance itself, but rather confidence in accurately judging emotional facial expressions is reduced with higher social anxiety trait levels (Folz et al., 2023). This observation is in line with general negative beliefs about one's performance in social situations, which are highlighted in cognitive models of social anxiety (Clark & Wells, 1995). Importantly, altered facial emotion perception has been linked to social interaction difficulties in both social anxiety (Gilboa-Schechtman & Shachar-Lavie, 2013) and autism (Boraston et al., 2007; D. A. Trevisan & Birmingham, 2016), which calls for an identification of potential underlying mechanisms.

Physiological Resonance of Perceived Facial Emotions

Facial emotional expressions are known to elicit physiological responses in an observer (Dimberg, 1982), and can form part of an "embodied simulation" of the corresponding emotional state (Niedenthal, 2007). Most research to date has focussed on the mirroring of facial expressions, so-called facial mimicry, and its role in processing others' emotions (Wood et al., 2016). Distinct mimicry patterns of various emotional expressions have been identified in neurotypical individuals (Wingenbach et al., 2020). Corresponding to the distinct facial muscle activation patterns in response to others' emotional facial expressions, researchers have aimed to identify consistent changes in autonomic activity that could reflect an embodiment of others' emotions. A clear physiological signature of perceiving distinct (facial) emotional expressions could, however, not be identified (Folz et al., 2022). Indexing sympathetic activity, skin conductance has been highlighted as a measure to validly reflect changes in experienced emotional arousal, independent of valence (Ventura-Bort et al., 2022).

Alterations in Facial Mimicry in Autism and Social Anxiety

Research on mimicry of emotional facial expressions has revealed these automatic facial muscle responses to be reduced in individuals on the autism spectrum compared to neurotypical individuals (Davies et al., 2016). Importantly, the general facial expressiveness or the ability to mimic expressions voluntarily has not been described to be altered in autism (Rozga et al., 2013; Weiss et al., 2019), even though speed and precision of the latter might be decreased (Drimalla et al., 2021). Next to alterations in facial mimicry itself, it has recently been suggested that automatic simulations of others' expressions might be less strongly integrated in emotion processing in autism (Folz et al., 2023).

Only few studies have investigated potential alterations of facial mimicry associated with social anxiety, and yielded inconclusive findings: some have reported no differences in sub-clinical individuals with higher levels of social anxiety traits (Dijk, Fischer, et al., 2018), but others have found enhanced mimicry of negative expressions, such as anger (Dimberg, 1997; Vrana & Gross, 2004) or disgust (Peter-Ruf et al., 2017). An enhanced mimicry of polite smiles has also been described in individuals with high social anxiety traits in a real social context (Dijk, Fischer, et al., 2018). Mimicry of genuine smiles, however, has not been observed to be enhanced in this study, and has even been found to be reduced in computer-based tasks (Dimberg, 1997; Vrana & Gross, 2004). Thus, individuals with social anxiety might rather mimic smiles more strongly in interaction with others as social signals and not as an enhanced simulation.

Alterations in Emotional Arousal in Autism and Social Anxiety

Differences in terms of both hyper- and hypoarousal have been proposed in autism in an emotion processing context, with an individual's arousal profile (i.e., hypo- or hyperarousal) supposedly depending on their attentional deployment tendencies (Cuve et al., 2018). Studies have, however, only reported reduced arousal in individuals on the autism spectrum compared to neurotypical individuals when the expressor's emotional state explicitly had to be judged (Hubert et al., 2009). No differences in objective arousal measures have been found when emotional facial expressions (Mathersul et al., 2013) or videos of social emotional scenes (Dijkhuis et al., 2019) were solely viewed, although individuals on the autism spectrum reported to be less emotionally affected by the videos compared to neurotypical individuals. Thus, it is yet to be determined how own physiological arousal influences the processing of other's emotion in autism.

Paralleling the limited research on facial mimicry, only few studies have measured autonomic nervous system responses during facial emotion perception in social anxiety and results are not conclusive. Although one might expect higher arousal responses to negative and, perhaps, neutral facial expressions based on the general negativity bias, most studies have found no differences between high and low socially anxious individuals in skin conductance responses during facial emotion perception (Dimberg & Thunberg, 2007; Merckelbach et al., 1989). Yet, there is some evidence for relatively lower responses in skin conductance to positive and higher responses to negative expressions in high versus low socially anxious individuals (Tsunoda et al., 2008; Vrana & Gross, 2004). It, however, remains unknown whether potentially altered autonomic responses have an impact on the judgments of others' emotions in social anxiety.

Integration of Physiological Resonance in Facial Emotion Perception in Autism and Social Anxiety

In both social anxiety and autism, a mismatch between objectively measured and subjectively reported physiological responses have been observed (Dijkhuis et al., 2019; Nikolić et al., 2015). As interpretations of others' facial expressions can be informed by those responses, not only their actual magnitude but also (a) their accurate sensation; and (b) the attention to those signals are important to consider in explaining facial emotion perception alterations in autism and social anxiety. Research on interoception, which describes the sensation, integration, interpretation and regulation of internal signals (Chen et al., 2021), has revealed that physiological signals are objectively sensed less accurately by individuals on the autism spectrum compared to neurotypical individuals (Failla et al., 2020; Garfinkel et al., 2016). While distinct body sensations are subjectively overperceived (Garfinkel et al., 2016), individuals on the autism spectrum report difficulties in the integration of different sensations and their interpretation (Fiene et al., 2018; T. R. Hatfield et al., 2019). Reduced interoceptive accuracy in autism has already been linked to reduced empathy in past research (Mul et al., 2018), yet not consistently (Butera et al., 2023), which highlights the importance of exploring this potential influence on perceiving others' emotions more strongly.

Although objectively not differing from individuals without social anxiety in their physiological responses, individuals with social anxiety have reported to perceive their own bodily arousal more strongly in social settings (Edelmann & Baker, 2002; Nikolić et al., 2015; Shalom et al., 2015), suggesting a higher interoceptive attention. Studies which objectively assessed the sensation of one's heartbeat (i.e., cardiac interoception) have yet described a reduced accuracy in individuals with social anxiety compared to control participants (Gaebler et al., 2013) or found no group differences (Antony et al., 1995). In how far alterations in perceiving one's own physiological signals relate to altered perception of other's emotions in social anxiety is still to be determined.

Objectives of the Current Study

The goal of the current study was to investigate putative alterations in the role that physiological feedback might have in facial emotion processing in autism and social anxiety. Hence, we first measured automatic changes in facial muscle activity (i.e., facial mimicry) and in skin conductance while participants were passively viewing spontaneous and standardized videos of facial emotional expressions. In a separate task, participants were asked to label each viewed expression according to five categories, to indicate their confidence in correctly labelling the expression, and to judge its emotional intensity. These measures allowed us to test whether sensorimotor simulations of some facial expressions and/or changes in arousal would be differentially predictive of (a) correctly recognizing an expression; (b) confidence in one's performance; and (c) judging the intensity of another person's emotional experience in individuals on the autism spectrum or with social anxiety compared to matched control participants. Based on the assumption that individuals on the autism spectrum would have a more noisy integration of physiological signals in higher level processing (Van de Cruys et al., 2017), we expected to observe a weaker link between emotion recognition accuracy and facial mimicry in autism, while, at the same time, both emotion recognition accuracy and facial mimicry would be reduced compared to the matched neurotypical controls. In those lines, we also explored if the link between emotional intensity judgments and autonomic arousal, indexed by changes in skin conductance, would be less strong in individuals on the autism spectrum compared to neurotypical controls. In individuals with social anxiety, in contrast, we did not expect to see differences in the magnitude of physiological responses and in emotion recognition accuracy, and neither in their link, compared to the control group, as we did not provide a real social setting. Yet, as reflection of negative beliefs about one's social skills, confidence in emotion recognition was expected to be overall reduced in individuals with social anxiety compared to controls, and especially negative and neutral facial expressions were expected to be judged more emotionally intense, in line with the negativity bias. Here, we aimed to explore whether the link between confidence and/or intensity judgments and physiological responses might be modulated, which might be linked to known misperceptions of physiological arousal. On top of that, by including self-reported interoception in our study, we could further explore whether individuals on the autism spectrum or with social anxiety also report differential accuracy in sensing their bodily signals, or differences in attention towards them, in daily life, potentially accounting for observed effects in our emotion processing context.

Methods

Participants

In total, the sample comprised 107 participants (65 women) within the age of 19-62 years (M_{age} = 34.82, SD = 12.31) who were divided in three subgroups: 40 individuals were on the autism spectrum (AS group, 28 women, M_{age} = 36.90, SD = 12.52), 27 individuals were diagnosed with clinically relevant social anxiety (SA group, 15 women, M_{age} = 31.89, SD = 10.43) and the remaining 40 neurotypical individuals had no history of Axis I DSM-5 diagnoses (NC group, 22 women, M_{age} = 34.73, SD = 13.12). All participants were native speakers of German living in Germany. Exclusion criteria for all groups were history of illegal drug use, alcohol abuse or addiction, serious head injuries, neurological or other severe internal conditions. Control participants with any first-degree relatives with a history of mental disorders were excluded from the study. An overview for existing comorbidities that did not lead to exclusion can be found in Table S1 in the Supplemental Material. In addition to being matched for gender and age on a group level, we also ensured that the groups did not significantly differ in their level of education, indexed by the years of education (AS group: M = 17.68, SD = 5.24; SA group: M = 16.48, SD = 2.92; NC group: M = 16.7, SD = 3.29) and intelligence indexed by the Multiple Choice Vocabulary Intelligence Test (MWT-B; Lehrl, 2005; see Supplemental Materials for additional information). Group differences in diagnostic and self-reported trait variables are outlined in Table S3 in the Supplemental Material.

Clinical participants were recruited from different in- and outpatient units in the LVR-University Hospital in Essen. Moreover, nearby therapy centres as well as patient groups (e.g. support groups, online forums) were contacted. Newspaper and online advertisements (e.g., of the Scientific Society Autism Spectrum WGAS) were published. The sample size was determined based on a power analysis using the simr package in R (P. Green & MacLeod, 2016). More specifically, we used an observation from our previous study in a student sample as basis, namely lower confidence in general emotion recognition with higher social anxiety trait levels (β = - 0.13, Folz et al., 2023). A sample size of 40 participants was deemed sufficient to detect a medium effect (-0.5) with 100% power and a small effect (-0.26) with 77% power. Importantly, this power analysis covered one specific effect and we only managed to recruit 27 individuals with social anxiety during the study period (September 2021 – October 2023, including the COVID-19 pandemic). Therefore, we decided to additionally employ Bayesian analyses to identify whether our sample was large enough to find convincing evidence for the alternative or null hypothesis in our group comparisons of interest.

Written consent was obtained from all participants prior to participation. The current study was part of a larger research project including additional tasks and measurements (see Procedure section), which encompassed two testing days of 2-2.5 hours duration each. After completion of all tasks on the second testing day, participants were given verbal and written debriefing about the study and received a fixed reimbursement of 50€ for their travel costs and varying bonus payments depending on outcomes in another task (0 – 2.5€). The design of the study was approved by the Medical Ethics Committee Leiden The Hague Delft (NL67766.058.18) and the Ethics Committee of the Medical Faculty of the University of Duisburg-Essen (19-8732-BO).

Stimuli

Eight identities (four women) displaying anger, fear, happiness, sadness, and neutral expressions were chosen as a source of stimuli from the FEEDTUM database(Wallhoff et al., 2006), which includes videotaped non-instructed reactions to emotion-inducing video-clips, resulting in spontaneous and hence more naturalistic expressions than acted emotional stimuli. The selected videos were standardized so that each clip had a duration of two seconds which included a neutral expression of 500ms followed by 1500ms of each category's expression, placed in front of a uniform grey background (for the selection and standardization procedure, see Folz et al., 2023). In sum, the stimulus set contained 40 two-second videos, depicting five emotion categories by eight individuals.

Procedure

The general procedure consisted of two separate days. On the first testing day, participants underwent multiple diagnostic assessments and filled in various questionnaires in addition to the questionnaires of interest, which are described in more detail and summarized in the Supplemental Materials in Table S3. The second testing day was scheduled within the following seven days. After being briefed on the procedure, electrodes were attached to the participants' faces (see Facial Electromyography section) and hands (see Skin Conductance section). Participants were positioned at a distance of 50cm from a Philips screen with a resolution of 1920x1080 pixels. Using E-Prime 3.0 software, the stimuli (720 x 480 pixels) were presented in the center of the screen. The study consisted of two consecutive subtasks. In the first task, participants were instructed to observe the stimuli without engaging in any action while psychophysiological and video data was recorded. Each trial began with the appearance of a black fixation cross on a grey background, lasting for one second, followed by the presentation of one of the 40 video stimuli for two seconds. To mitigate potential data inaccuracies arising from background noise, each participant watched each of the 40 videos twice, resulting in a total of 80 trials. The task had a duration of approximately 20 minutes.

Upon completion of the first task, the electrodes were removed from the participants' faces, and the second subtask (emotion labelling) commenced. All 40 video sequences were once again presented, totaling three viewings per participant. When the video clip disappeared, participants were asked to judge the displayed expression. Specifically, we asked the following questions: (a) "What type of expression was exhibited by the person in the video?"; (b) "How confident are you in your judgment?" (ranging from "not confident at all" to "very confident"); and (c) "How emotionally intense was the expression portrayed in the video?" (ranging from "not intense at all" to "very intense"). Participants used horizontal sliders with invisible values to indicate their responses, ranging from 0 to 100 with increments of 10. The second subtask lasted approximately 10 minutes.

Measurements

Facial Electromyography (fEMG)

Following the guidelines of Fridlund and Cacioppo (1986), we applied reusable 4 mm Ag/AgCl surface electrodes on the left side of the participants' faces to measure facial electromyography (fEMG). Two electrodes were placed over the Corrugator Supercilii region (referred to as "corrugator" hereafter) to measure facial muscle (de-)activations that form part of mimicry patterns, which have been described for happy, sad, fearful, and angry expressions (Künecke et al., 2014). As another part of the facial mimicry pattern of happy expressions, facial muscle activations over the Zygomaticus Major region (referred to as "zygomaticus" hereafter) were measured with two additional electrodes. The ground electrode was applied on the top of the forehead. A Biopac MP160 system combined with a BioNomadix 2 channel wireless EMG amplifier was used to transmit and amplify the signals, which were recorded in AcqKnowledge 5.0 (Biopac Systems Inc, 2009) with a sampling rate of 1000 Hz. Initial data inspection and preprocessing was performed in the PhysioData Toolbox v.0.6.3 (Sjak-Shie, 2019), including rectification, filtering (28 Hz high cut-off filter, 500 Hz low cut-off filter and 50 Hz notch filter) and smoothing (Boxcar filter with 100ms window size). Based on the initial data inspection and the notes that had been taken during the recordings, corrugator data of six participants and zygomaticus data of five participants were entirely excluded due to poor data quality. Furthermore, the time-locked videos belonging to each datafile were carefully inspected for perturbations simultaneously with the EMG data recordings, and trials with visible effects on the data during stimulus presentation were noted for exclusion (corrugator: 277 trials, 3.4%; zygomaticus: 363 trials, 4.4%). After exporting the EMG signals for each trial, which were downsampled to 10 Hz, a baseline correction was performed. Here, the mean signal of the first 500ms of stimulus presentation, in which the expression was still neutral, served as baseline and was subtracted from each datapoint of the following 1.5s belonging to the same trial, in which the emotional expression developed. The data during the last second of the stimulus presentation in which the full emotional expression was shown (ten datapoints) was then averaged for each participant and each muscle region across the two presentations of each of the 40 distinct stimuli.

Skin Conductance

Two electrodes were attached to the index finger and the ring finger of the participants' non-dominant hands to measure changes in skin conductance (SC). The signal was transmitted using the same Biopac MP160 system as for the fEMG recordings with an EDA100C module (settings: 2000 Hz sampling rate, Gain: 10μV, 1 Hz low-pass filter) and all physiological recordings were stored in the same AcqKnowledge datafile. The SC data was also preprocessed in the PhysioData Toolbox v.0.6.3 (Sjak-Shie, 2019), by applying the same visual inspection procedure as for the fEMG data. Due to poor data quality, six participants had to be entirely excluded, as well as a total of 313 trials (3.9%) of the remaining participants. Similar to the fEMG data, the downsampled SC data (10Hz) was then baseline-corrected for each trial. Based on previous research (Tsunoda et al., 2008), we decided to consider the maximum positive deflection in the baseline-corrected signal up until four seconds after emotion onset (i.e., a 5.5s time window) as peak response to the stimulus, and eventually log-transformed the distribution after adding 1 as a constant to each data point.

Questionnaires

Descriptions of the completed questionnaires which were not outcome measures in our analyses are summarized in the Supplemental Material, including descriptive statistics by group and group comparisons (see Table S3). In the following, more detailed information about the questionnaires of interest for the current study is provided.

Interoception measures. Two self-report questionnaires were used in order to measure subjective perceptions of interoceptive accuracy and attention:

the German versions (Brand et al., 2023; Tünte et al., 2023) of the Interoceptive Accuracy Scale (IAS; Murphy et al., 2020), and the Interoceptive Attention Scale (IATS; Gabriele et al., 2022). The IAS evaluates subjective beliefs regarding one's capability to accurately perceive interoceptive signals, whereas the IATS assesses subjective beliefs concerning one's attention to interoceptive sensations. Participants judge internal body states of 21 bodily signals (e.g., heartbeat, pain, need to urinate) rated on a scale from 1 = strongly disagree to 5 = strongly agree, with scores ranging from 21-105. Higher scores indicate greater self-reported interoceptive accuracy or attention. With an alpha of .88 (95% CI [.84, .91]) and .89 (95% CI [.86, .92]), respectively, both the IAS and the IATS showed good internal consistency in our sample.

Data Analysis

The main interest of this study was to examine potential alterations in the link between physiological measures and facial emotion perception reports in autism and social anxiety. First, we conducted simple group comparisons on alterations in physiological responses and facial emotion perception reports on subject-level averaged data, as well as on alterations in interoception self-reports. Due to unequal sample sizes and variances in the three groups, we first ran a Kruskal-Wallis test as omnibus test, which was followed by Wilcoxon rank sum tests (each clinical group against NC), using the Benjamini Hochberg correction for multiple comparisons. Prior to model fitting for the main analysis on a trial-by-trial level, self-reported *Confidence in Emotion recognition accuracy* and *Perceived emotional intensity* were standardized (i.e., centered and scaled) to facilitate model coefficient interpretation. As mimicry of different emotional facial expressions involves distinct muscle regions (see fEMG section), we fitted separate models to investigate alterations in the association between facial muscle responses and emotion perception of specific facial expressions. All negative expressions were included in the same models, together with the neutral expression, as they have all been linked to increased corrugator activity in past research. The variables *Emotion category* (anger, fear, sadness and neutral), *Corrugator activity* (baseline-corrected and z-scored), and *Group* (AS, SA, NC), as well as their two-way interactions (*Emotion category*Group* and *Corrugator activity*Group*) and the three-way interaction (*Emotion category*Corrugator activity*Group*), were thus predictors in (Generalized) Linear Mixed Models (GLMMS) with (1) *Emotion recognition accuracy* (binomial, 1 = correct/0 = incorrect), (2) *Confidence in emotion*

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recognition (eleven ascending values, treated as continuous) and (3) *Perceived emotional intensity* (eleven ascending values, treated as continuous). Happy facial expressions were recognized at ceiling performance in all three groups (overall <1% inaccurate responses, see also Table S2), resulting in little variance in *Emotion recognition accuracy* to predict. As a consequence, we investigated how both activity over the corrugator region and zygomaticus region, which tends to be decreased and increased, respectively, when mimicking happy expressions, would differentially relate to the confidence in the recognition of the expressions as well as their perceived emotional intensity but not emotion recognition accuracy. Hence, *Corrugator activity* (baseline-corrected and z-scored), *Zygomaticus activity* (baseline-corrected and z-scored) and *Group* (AS, SA, NC), as well as both two-way interaction between one muscle region and group, became predictors of (4) *Confidence in emotion recognition* of happy expressions and (5) *Perceived emotional intensity* of happy expressions in two separate LMMs. The addition of a three-way interaction (*Corrugator activity*Zygomaticus activity*Group*) did not improve either model fit. Lastly, as changes in skin conductance in response to emotional stimuli have been shown to reflect emotional arousal in general rather than being emotion-specific, the three final (G)LMMs of the main analysis included all emotional expressions, with the exception of the at ceiling recognized happy expressions in the *Emotion recognition accuracy* model. We thus predicted (6) *Emotion recognition accuracy*, (7) *Confidence in emotion recognition* and (8) *Perceived emotional intensity* by *Emotion category* (anger, fear, happiness (not in accuracy model), sadness, neutral), *Skin conductance* (log-transformed maximum deflection) and *Group* (AS, SA, NC), as well as their two-way interactions and the three-way interaction.

Based on research highlighting the role of alexithymia in altered interoception (e.g., Brewer et al., 2016) and emotion processing (D. A. Trevisan & Birmingham, 2016) as well as on observing significant group differences in depressive symptoms (see Table S2), we re-fitted all models with standardized alexithymia and depressive symptom scores as covariates, which did not change our results in a meaningful way. As mentioned above, we additionally fitted Bayesian mixed models to have more certainty not only with regard to the alternative but also the null hypothesis. To evaluate the independence of observations on prior specifications, we fitted models with narrow (normal(0, 1)), medium (normal(0, 2.5)) and wide (normal(0, 5)) priors. All statistical analysis were conducted in R 4.2.2. More technical details regarding the analyses can be found in the Supplemental Materials.

Results

Group Differences in Physiological Resonance, Facial Emotion Perception, and Interoception

In line with previous work, we observed a reduction in automatic facial mimicry responses to happy facial expressions, as well as a less accurate and confident emotion recognition, in individuals on the autism spectrum. More specifically, less relaxation of the corrugator in response to happy expressions was observed in the AS group compared to the NC group, p = .001, effect size r = 0.39. Furthermore, compared to the NC group, individuals on the autism spectrum were less accurate in the recognition of fearful expressions, p < .001, effect size r = 0.47, and of sadness expressions, p = .001, effect size r = 0.39. An overview of misclassifications to specific emotion categories can be found in Figure S1 in the Supplemental Materials. The ceiling performance for happy expressions in both the NC group and the SA group did not allow for group comparisons (100% accuracy rates). Individuals on the autism spectrum also reported reduced confidence in the recognition of all facial expressions compared to the NC group ($ps_{emotions}$ < .001, range effect size r: 0.45 – 0.48 and $p_{neutral}$ = .002, effect size r = 0.36). Lastly, the intensity of both angry and fearful expressions was perceived as less emotionally intense in the AS group compared to the NC group, p = .021, effect size r = 0.29 and p = .021, effect size r = 0.37 respectively (see Figure 1 and Table S2 in the Supplemental Material for an overview of all group differences).

Additionally, both clinical groups reported to be less accurate in the perception of their interoceptive signals (SA group: p = .002, effect size r = 0.37; AS group: p < .001, effect size r = 0.42) while attending more strongly to them in everyday life (SA group: p < .001 effect size r = 0.45; AS group: p = .010, effect size r = 0.29).

Facial Muscle Activity and the Perception of Negative Facial Expressions

Against our expectations, we did neither observe a significant three-way interaction between *Emotion category*, *Corrugator activity* and *Group*, nor a significant two-way interaction between *Corrugator activity* and *Group* in the model with *Emotion recognition accuracy* as outcome (see Table S4 in the Supplemental Material for the model fit). Thus, there was no evidence for differences in the relation between activity over the corrugator muscle region (“frowning”) and recognition of (specific) negative emotional expressions between

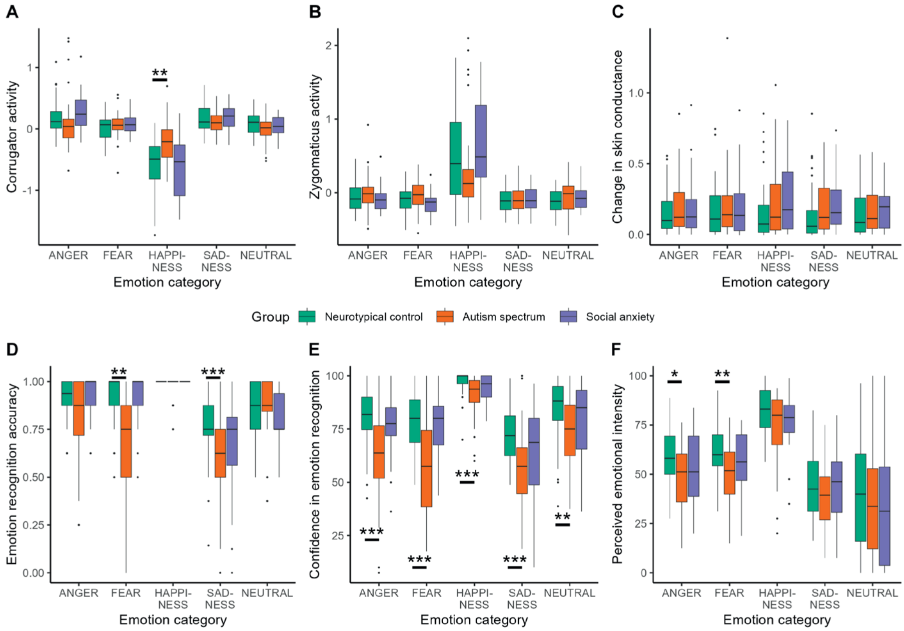

Figure 1. Group differences in physiological measures and facial emotion perception judgments. Graphs depict differences on subject-level averaged data by emotion category in (A) baseline-corrected, z-scored corrugator activity, (B) baseline-corrected, z-scored zygomaticus activity, (C) baseline-corrected, log-transformed maximum deflection in skin conductance, (D) emotion recognition accuracy, (E) confidence in emotion recognition, and (F) perceived emotional intensity. Significant group differences in Wilcoxon rank sum tests are indicated by asterisks, according to the significance levels: *** p < .001; ** p < .01, * p < .05.

with Bayes factors below 0.3 supporting the null hypothesis, apart from the NC-SA difference for fearful expression (0.48). Yet, next to main effects of *Emotion category* and *Group*, we observed significant interactions between *Emotion category* and *Corrugator activity*, $\chi 2 = 9.62$, $p = .022$, as well as between *Emotion category* and *Group*, $\chi 2 = 46.57$, $p < .001$. In line with the results on the subject-level averaged data, recognition of sadness and fear displays was significantly less accurate in the AS group compared to the control group, $OR_{Sadness} = 0.40$, 95%CI [0.23 ,0.71], $p <$ .001 and $OR_{Fear} = 0.15$, 95%CI [0.08, 0.30], $p = .001$. We additionally observed worse recognition of angry facial expressions in the AS compared to the NC group, $OR = 0.43$, 95%CI [0.22, 0.85], $p = .011$. Similarly, we only found group differences in rating both *Confidence in emotion recognition* and *Perceived emotional intensity*, independent of *Corrugator activity*, for the different levels of *Emotion category* $F(6,3275) = 5.32$, p <.001 and $F(6,3275) = 4.69$, p <.001 respectively (see Tables S5 and S6 in the Supplemental Material for the model fits). Looking at the Bayes factors, there indeed seemed to be evidence for no differences in the association between *Corrugator activity* with *Confidence in emotion recognition* between groups (BF range: 0.08 – 0.15), apart from the comparison of angry expressions between the AS group and the NC group, for which the evidence was inconclusive (BF = 0.58). For *Perceived emotional intensity* as outcome, in contrast, robust evidence for a difference between the AS and NC group could be found across prior specifications for angry expressions (BF = 12.76 at a medium prior), and less robust evidence for a difference between the SA and NC group (i.e., BF > 3 only at a narrow prior) (see Figure 2). The Bayes factors for the slope comparison against zero for each group suggested that slope differences between groups mainly seemed to be driven by a robust positive relation between *Corrugator activity* and *Perceived emotional intensity* in the NC group, however only when specifying a narrow prior (BF = 4.94), and not medium (BF = 2.19) or wide (BF = 1.24) priors. Bayes factors for the group comparisons of all other expressions were very low, thus in favour of the null hypothesis (BF range: 0.05 – 0.10).

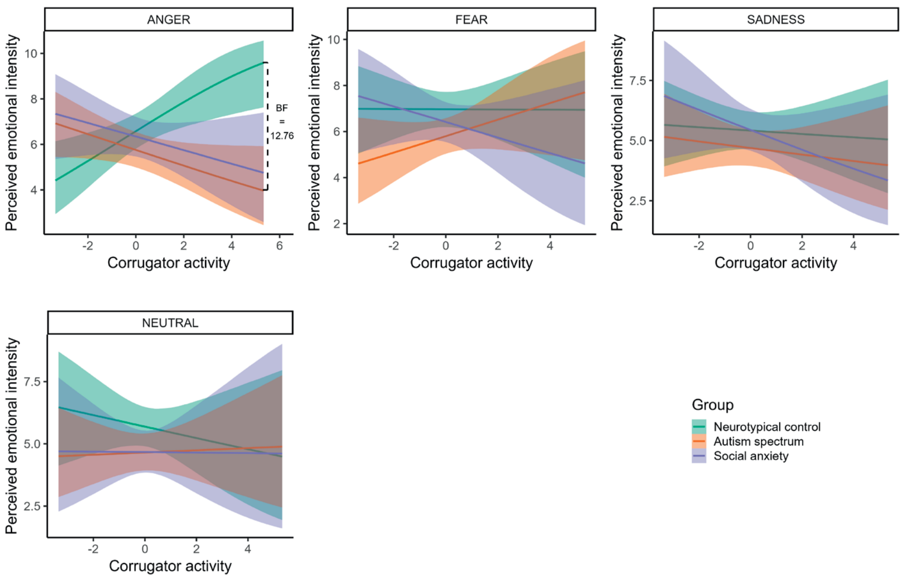

Figure 2. Group differences in the relation between baseline-corrected, z-scored corrugator activity during the viewing of negative and neutral facial expressions and their perceived emotional intensity (rescaled to an ordinal scale of 0-10) by expression category, as observed in the Bayesian analysis. Robust evidence for group differences is indicated by a bracket, including the corresponding Bayes Factor.

As already indicated in the preliminary analysis, *Confidence in emotion recognition* was significantly reduced for all expressions in the AS group compared to the NC group (estimate range: -0.77 to -0.41, most p < .001 apart from neutral: .002). Moreover, the autism group rated specifically fearful and angry expressions as less intense compared to the NC group, estimate = -0.39, 95% CI[-0.67, -0.11], z = -3.13, p = 0.004 and estimate = -0.32, 95% CI[-0.60, -0.04], z = -2.60, p = 0.019, whereas no significant differences in *Perceived emotional intensity* ratings were observed between the SA and the NC group.

Facial Muscle Activity and the Perception of Happy Facial Expressions

Similar to the models on the perception of negative facial expressions, we did not observe alterations in the link between activity in either facial muscle region and *Confidence in emotion recognition* of happy expressions as well as their *Perceived emotional intensity* (see Table S7 and S8 in the Supplemental Material for the model fits). Bayes factors of group comparisons ranged between 0.07 and 0.32, supporting the null hypothesis. There were only overall *Group* differences in the *Confidence in emotion recognition,* F(2,139) = 9.23, p <.001. Namely, the AS group showed to be less confident in accurately labelling happy expressions, β = - 0.47, 95%CI [-0.73, -0.22], t(108.46) = -3.67, p < .001, compared to the NC group.

Skin Conductance and the Perception of Facial Expressions

The model fits with *Emotion recognition accuracy* and *Confidence in emotion recognitio*n as outcomes did not show any significant effects associated with the predictor *Skin conductance* (see Table S9 and S10 in the Supplemental Material). Bayesian analysis confirmed that there was no robust support for alterations in the association between *Skin conductance* and *Emotion recognition accuracy* (BF range: 0.17 – 0.73) or *Confidence in emotion recognition* (BF range: 0.09 – 0.36) for all facial expressions, except for some anecdotal evidence in the AS-NC comparison for the accurate recognition of fearful expressions (BF = 1.83). As already reported in the previous models, *Emotion recognition accuracy* was found to be reduced for angry, fearful and sad expressions in the autism group compared to the neurotypical control group (see Table S9 in the Supplemental Material). Similarly, *Confidence in emotion recognition* was found to be reduced for all expressions, including the happy expression in this model, estimate = -0.30, 95%CI [-0.55,-0.05], z = -2.69, p = .014, in the AS group compared to the NC group (see Table S10 the Supplemental Material). Interestingly, when including all expressions in one model, *Confidence* *in emotion recognition* of sad expressions was not only reduced in the SA group compared to the NC group, estimate = -0.29, 95%CI [-0.58,-0.01], z = -2.30, p = .022, but they were also less well recognized, *OR* = 0.52, 95% CI [0.27, 1.00], z = -2.24, p = .025. Next to main effects of *Emotion category* and *Group* (see Table S11 in the Supplemental Material), we also observed a significant three-way interaction between *Emotion category*, *Skin conductance* and *Group* in the prediction of *Perceived emotional intensity*, $F(8,3883) = 2.20$, p = .025.

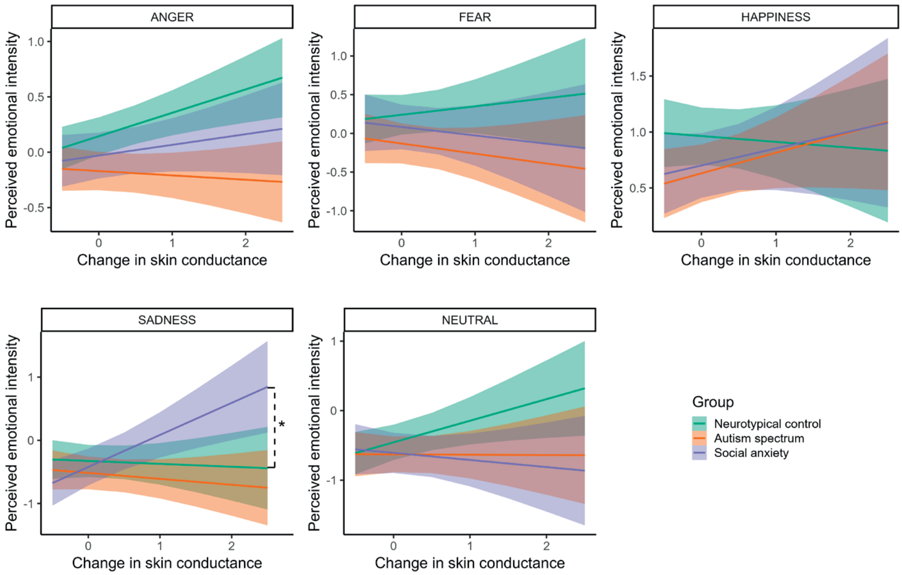

Figure 3. Group differences in the relation between baseline-corrected, log-transformed maximum change in skin conductance during the viewing of all facial expressions and their perceived emotional intensity (standardized) by expression category, as observed in the Frequentist analysis. The significant group difference in the slope comparison is indicated by an asterisk.

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Stronger increases in skin conductance in response to sad expressions were significantly associated with higher *Perceived emotional intensity* in the SA group compared to the NC group, estimate = 0.55, 95% CI [0.07, 1.03], $t(3914) = 2.60$, p = .019. Slope comparisons against zero further revealed that the slope of this relation in the SA group was significantly different from 0, estimate = 0.51, 95%CI [0.09, 0.93], $t(3915) = 3.11$, p = 0.001, while there was no evidence for the other groups or expressions (see Figure 3). The Bayesian analysis supported this observation of a greater slope than zero across prior specifications (BF range: 4.27 – 15.16), but robust evidence for slope difference between the SA and NC group was only found when specifying a narrow prior (BF = 4.15), and not medium (BF = 2.47) or wide (BF = 1.27) priors.

Exploratory: Altered Interoception as Potential Explanation to Alterations in the Link between Physiological Resonance and Perceived Emotional Intensity

Our analyses revealed that group differences only existed in the link between physiological measures and *Perceived Emotional Intensity*, and not *Emotion recognition accuracy* or the *Confidence* therein. Therefore, we focused on investigating whether self-reported interoception measures would account for these observed effects in our exploratory analyses. More specifically, both the Bayesian and Frequentist approaches indicated that stronger increases in skin conductance were more strongly (and even exclusively) associated with higher perceived emotional intensity ratings of sad facial expressions in individuals with social anxiety. Based on past findings as well as the increased interoceptive attention reports in the SA group in our study, we were interested to see whether the link in the SA group would change when accounting for differences in interoceptive attention in the link between *Skin conductance* and *Perceived emotional intensity* for the different expression categories. Hence, we re-fitted the model on *Perceived emotional intensity* of all expressions with the interactions including *Skin conductance* as predictor, and included another three-way interaction term between *Emotion category*, *Skin conductance and Interoceptive attention*, as well as the two associated two-way interactions and the main effect of *Interoceptive attention* (see Table S12 in the Supplemental Material for the model fit). The addition of *Interoceptive attention* (including its interactions with other predictors) did not change the effect of interest, namely that the association between *Perceived emotional intensity* of sad expressions and increases in skin conductance was positive (i.e., larger than 0) in the SA group, estimate = 0.53, 95%CI [0.10, 0.96], $t(3836) = 3.19$, $p = 0.007$, and significantly stronger compared to the NC group, estimate = 0.60, 95% CI [0.10, 1.11], $t(3867) = 2.68$, $p = .015$. These observations were confirmed by Bayes factors for the SA-NC group comparison (BF = 2.47) as well as the slope comparison against zero (BF = 7.99) which were similar in size to the model without *Interoceptive attention* for at a medium prior specification.

In the current study, we also observed that perceived emotional intensity in anger displays was more positively linked to *Corrugator activity* in the NC group compared to the AS group. This could be the result of neurotypical individuals accurately sensing changes in facial muscle configuration and integrating this information in their judgments, whereas lower interoceptive accuracy has been consistently found in individuals on the autism spectrum in past research as well as the current study, potentially resulting in less beneficial facial feedback. To test the role of *Interoceptive accuracy* in the link between *Corrugator activity* and *Perceived emotional intensity* of negative expressions, we re-fitted the model on *Perceived emotional intensity* of negative expressions with the interactions including *Corrugator activity* as predictor, and included another three-way interaction term between *Emotion category*, *Corrugator activity* and *Interoceptive accuracy*, as well as the two associated two-way interactions and the main effect of *Interoceptive accuracy* (see Table S13 in the Supplemental Material for the model fit). In this model, we observed a significant two-way interaction between *Interoceptive accuracy* and *Corrugator activity*, $F(1,3201) = 3.92$, $p = .048$, with the positive link between *Corrugator activity* and *Perceived emotional intensity* being more pronounced with higher *Interoceptive accuracy*, $\beta = 0.03$, 95%CI [0.00, 0.06]. As we only observed robust evidence for a difference between the NC and the AS group in the link between *Corrugator activity* and *Perceived emotional intensity* of angry expressions, we focused on changes in Bayes factors. At a medium prior specification, the group comparison of the slope dropped to a Bayes factor of 5.21 (versus 12.76 in the original model) and there was not even anecdotal evidence for a positive slope in the NC group (BF = 0.58). Hence, the addition of *Interoceptive accuracy* to the model seemed to have partially accounted for group differences in how strongly "frowning" related to perceiving an angry expression as more emotionally intense.

Discussion

The goal of the current study was to investigate alterations in the links between physiological responses to facial emotional expressions and emotion perception in individuals on the autism spectrum and individuals with social anxiety, compared to neurotypical individuals. Overall, we identified group differences in the links between physiological measures and perceived emotional intensity ratings, and not emotion recognition accuracy or the confidence therein. Most robust evidence was observed in the association between skin conductance deflections and emotional intensity ratings of sad expressions. That is, higher physiological arousal was only predictive of more intense sadness ratings in individuals with social anxiety. Moreover, using a Bayesian approach, we found evidence for a less pronounced positive link between corrugator activity and emotional intensity ratings in individuals on the autism spectrum compared to controls. This effect was driven by a positive relation between "frowning" and perceiving angry expressions as emotionally intense, for which there was only weak evidence in the control group. Our exploratory analyses support the idea that self-reported interoceptive accuracy, but not interoceptive attention, might account for group differences in the link between physiological resonance of emotional expressions and their perception. In the remainder of this discussion, we will elaborate on these key findings (see Figure 4 for a visualization).

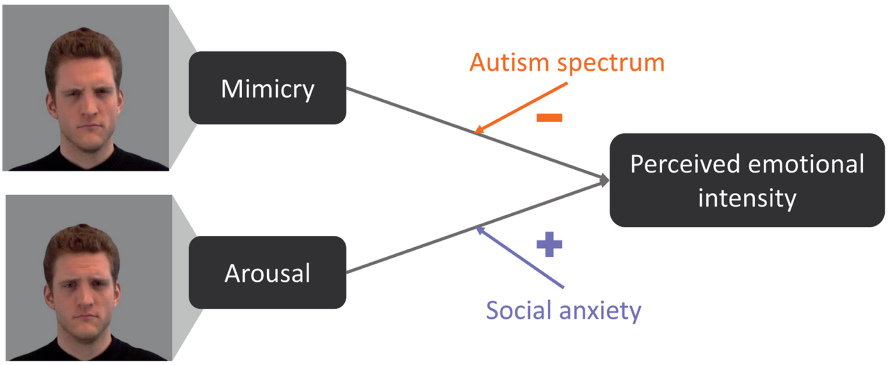


Figure 4. Visualization of significant alterations in the links between measures of physiological resonance and perceived emotional intensity. We used video stimuli which are based on the FEEDTUM database (Wallhoff et al., 2006). Permission to use the material under CC-by and to publish example images in scientific journals, such as in this figure, was granted to the first author of this study by the creators of the database.

Alterations in Physiological Resonance to Facial Emotions and Self-Reported Interoception

When exposed to a smile, people automatically mimic it: their zygomaticus muscle activates and their corrugator muscle correspondingly relaxes (Bourgeois & Hess, 2008). In the current study we observed that individuals on the autism spectrum showed a diminished relaxation of their corrugator muscle compared to the control group. Even though group differences in corrugator activity to happy expressions have rarely been the focus of previous research on facial mimicry in autism, similar observations of less relaxation have been made, yet not statistically tested (Rozga et al., 2013). In contrast to some existing findings on altered mimicry patterns in autism (Mathersul et al., 2013; Rozga et (Dimberg, 1997; Peter-Ruf et al., 2017; Vrana & Gross, 2004)al., 2017; Vrana & Gross, 2004), we did not observe group differences in zygomaticus activity to happy expressions as well as in corrugator activity to negative expressions. Importantly, this analysis was not the main focus of the study and we only looked at averaged data. Previous research suggests that differences between individuals on the autism spectrum and neurotypical controls might only become apparent in the latency, differentiation, or precision of mimicry responses (Drimalla et al., 2021; Oberman et al., 2009; Weiss et al., 2019). Furthermore, alterations in mimicry associated with social anxiety might be amplified in a real social context, in which the signaling function of facial expressions is met and social anxiety symptoms manifest (Dijk, Fischer, et al., 2018). Examining changes in skin conductance as an index of sympathetic activation, we did not observe any group differences in the magnitude of the response to all facial expression categories, replicating some existing findings in autism research (Mathersul et al., 2013) and social anxiety research (Dimberg & Thunberg, 2007; Merckelbach et al., 1989). The two clinical groups did, however, significantly differ from the control group in the self-reported interoception measures: both individuals on the autism spectrum and individuals with social anxiety described an increased interoceptive attention combined with a reduced interoceptive accuracy. An increased attention to bodily signals in individuals with social anxiety has mainly been reported in social situations and linked to a fear of displaying heightened arousal, such as blushing (Nikolić et al., 2015). Individuals on the autism spectrum, in contrast, have been found to report a stronger sensation of distinct body signals (Garfinkel et al., 2016), in line with a more general sensory hypersensitivity (Tavassoli et al., 2014), which might be bi-directionally linked to an increased interoceptive attention. Extending reports of reduced objectively-measured, cardiac interoceptive accuracy in individuals on the autism spectrum (Failla et al., 2020; Garfinkel et al., 2016; Mul et al., 2018), we also observed a lower self-reported interoceptive accuracy in autism. This goes along with the idea of highly inflexible precise prediction errors in autism (Van de Cruys et al., 2017), with various distinct body sensations as low level signals constantly being overrepresented. When aiming to retrieve specific information from their bodies, individuals on the autism spectrum might not be able to attenuate irrelevant signals and amplify the relevant signal against the noise, thus resulting in inaccurate judgments. Our observation of lower self-reported interoceptive accuracy in individuals with social anxiety is partially in line with the existing findings on objectively measured cardiac interoception: While one study found no differences in cardiac interoceptive accuracy in individuals with social anxiety compared to control participants (Antony et al., 1995), another study described a worse performance in the cardiac interoception task (Gaebler et al., 2013). A biased perception of physiological signals, namely an overperception of arousal, has been reported in previous social anxiety research (Edelmann & Baker, 2002). Possibly, an awareness of these biases may be reflected in decreased self-reported interoceptive accuracy.

Alterations in Facial Emotion Perception

In line with previous research, we observed lower emotion recognition accuracies in individuals on the autism spectrum compared to the control participants (Uljarevic & Hamilton, 2013; Yeung, 2022) as well as lower perceived emotional intensities (Schneider et al., 2020; Tseng et al., 2014). Contrasting past findings, confidence in the recognition of all facial expressions (including neutral) was also reduced in individuals on the autism spectrum compared to neurotypical controls (Sawyer et al., 2014; S. Wang & Adolphs, 2017). These lower confidence ratings might reflect the observed difficulties in labeling expressions, which might also be linked to perceiving less emotionality in them. Against our expectations, we did not observe reduced confidence in emotion recognition in individuals with social anxiety. There was only some evidence for lower confidence in the recognition of sad expressions, which was in line with their somewhat lower recognition rates. Although individuals with social anxiety are known to be negatively biased in forming beliefs about their social abilities (Koban et al., 2023; Müller-Pinzler et al., 2019), these beliefs might not manifest in a non-social setting such as in our experiment. Similarly, we did not observe a reflection of the proposed negativity bias in social anxiety (Chen, Short, et al., 2020; Machado-de-Sousa et al., 2010) in the subjective facial emotion perception measures, such as an improved recognition of negative expressions, higher misperception of neutral expressions or increased intensity ratings of expressions. While results from previous studies in sub-clinical individuals with varying social anxiety trait levels (Folz et al., 2023; Torro-Alves et al., 2016) as well as in clinical samples (Bui et al., 2017) suggest that the negativity bias might not impact the correct labeling of expressions per se, we would have expected to see an indication of a heightened sensitivity to negative social signals in the perceived intensity ratings. Importantly, participants were already exposed to each expression twice prior to rating it, which might have diminished negatively biased processing (Staugaard, 2010). We did, however, find evidence that the automatic physiological resonance of some expressions was differentially linked to how intensely they were perceived in the two clinical groups compared to the control group.

Alterations in the Link between Physiological Resonance and Facial Emotion Perception, and the Role of Interoception

Next to observing reductions in mimicking happy facial expressions as well as in facial emotion perception more broadly, we also found evidence for a weaker link between the mimicry and the perceived emotional intensity of angry expressions in individuals on the autism spectrum compared to neurotypical controls. Initially, we expected that a weaker link between physiological resonance and facial emotion perception in autism would become apparent in the prediction of emotion recognition accuracy, rather than perceived emotional intensity (Folz et al., 2023). Nevertheless, the direction of the effect was in line with our expectations, namely that higher corrugator activity was more strongly linked to perceiving angry expressions as more emotionally intense in neurotypical individuals compared to individuals on the autism spectrum. Although we cannot infer causality from our analysis, we suggest, based on theoretical frameworks as well as previous research that the simulation of expression-congruent muscle activations can boost emotion perception in others (Niedenthal et al., 2010; however see Holland et al., 2020). This embodied path to emotion perception might, in contrast, not be as strongly pronounced in individuals on the autism spectrum as in neurotypical individuals. One relevant variable in this path might be the ability to accurately sense signals from the body, reflected in measures of interoceptive accuracy (Arnold et al., 2019). When accounting for self-reported interoceptive accuracy in the link between corrugator activity and perceived emotional intensity of angry expressions, evidence for differences between individuals on the autism spectrum and neurotypical individuals was less robust, yet still present. A closer examination of the role of interoceptive accuracy in integrating signals from one's own body in perceiving others' emotion might thus be promising in gaining further insights in altered facial emotion perception in autism.

Individuals with social anxiety, in contrast, showed a more pronounced positive link between changes in skin conductance and perceived emotional intensity of sad expressions than the control participants. Specifically for sad expressions, mimicry of autonomic responses has been shown to influence facial emotion perception (see Critchley, 2009). As bodily arousal is typically overperceived in social situations by individuals with social anxiety (e.g., Shalom et al., 2015), increased attention to changes in skin conductance in response to sad expressions might explain the stronger link with intensity ratings. However, when including self-reported interoceptive attention in the analysis, there was no indication that it would account for the group differences. An alternative explanation could be that the link between physiological arousal and perceived intensity was more strongly pronounced in the social anxiety group compared to the control group because they had more difficulties in identifying sad expressions, as reflected in the decreased confidence and recognition rates. Similar to claims on the role of facial mimicry in processing observed emotional expressions (e.g., Wood et al., 2016), autonomic feedback, such as changes in skin conductance, might specifically inform facial emotion perception if expressions are ambiguous in the eyes of the perceiver. Whether the ambiguity of emotional expressions could indeed explain differences in how physiological signals relate to facial emotion perception should be investigated in future research.

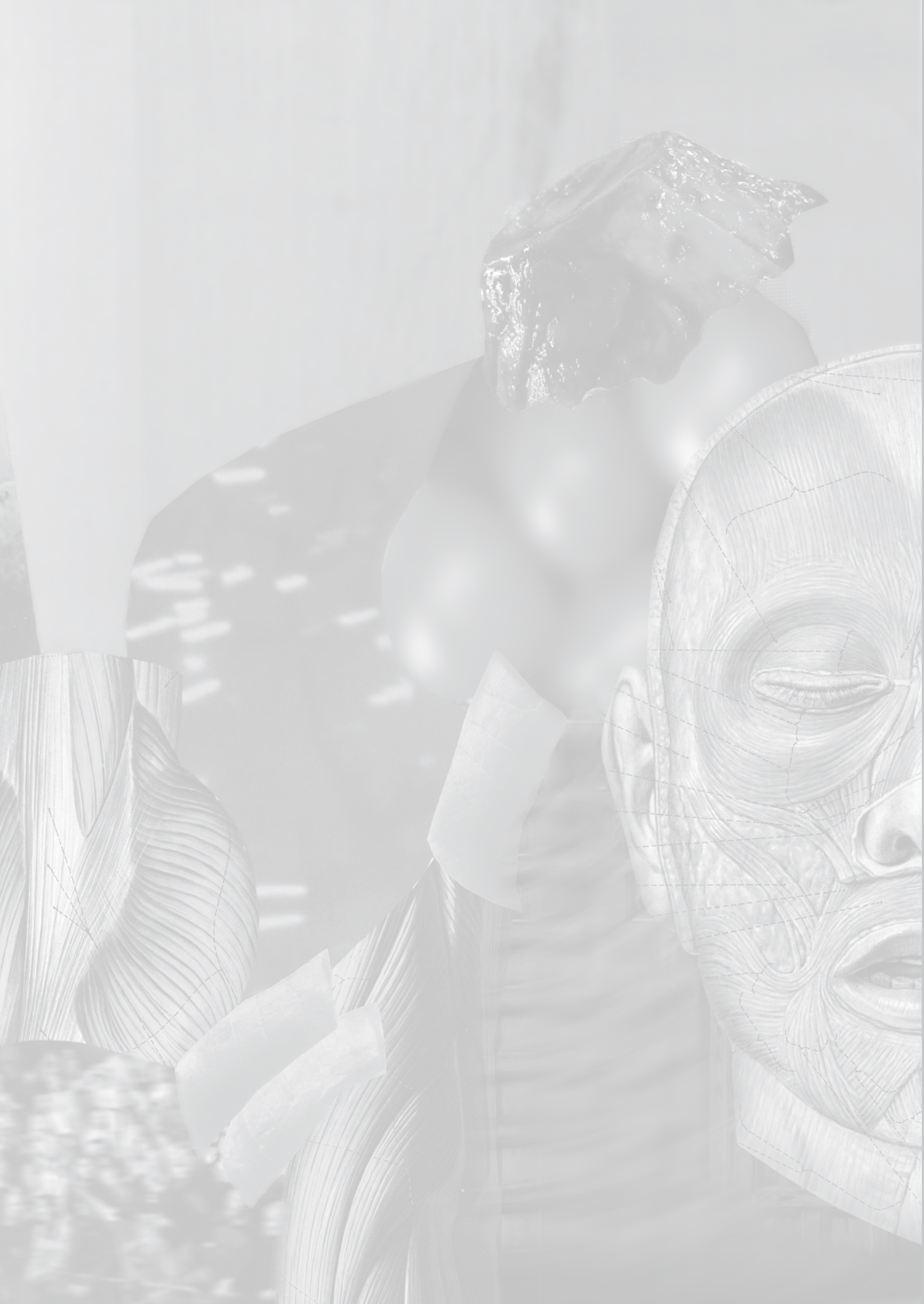
Limitations

While the current study provides valuable contributions to existing research on facial emotion perception, physiological resonance of facial expressions and interoception in autism and social anxiety, and additionally provides novel insights in condition-specific modulations in their relations, some limitations should be highlighted. One limitation is that we can only assume that physiological changes would inform facial emotion perception based on previous research (e.g., Critchley et al., 2005) but we could not infer causality in our study. This general shortcoming of studies relating co-occurrent changes in physiology to subjective reports (Olszanowski et al., 2020) has recently been addressed in novel approaches, such as directly manipulating facial muscle activity via facial neuromuscular electrical stimulation (Efthimiou et al., 2023). Thereby, alterations in processing and integrating physiological signals could also be further disentangled from alterations in physiological reactivity within the channel of interest. In those lines, the role of interoception in alterations in emotion perception should be more thoroughly investigated. In our study, we assessed group differences in interoception by using broad, high-level and belief-based measures whereas most previous studies assessed interoceptive accuracy objectively instead of or in addition to self-reports (Gaebler et al., 2013; Garfinkel et al., 2016). Crucially, in order to fully understand individual differences in interoception, a more comprehensive assessment has been called for, across different dimensions and bodily axes (Suksasilp & Garfinkel, 2022).

The generalizability of our results is additionally limited by the heterogeneity within the clinical conditions (e.g., see comorbidities in Table S1 in the Supplemental Materials), by the unequal gender distribution, as well as by the relatively low ecological validity. For example, differences in processing social signals in social anxiety might be further emphasized by alterations in behaviour in real social situations, such as attentional avoidance of social signals (Konovalova et al., 2021). Lastly, it should be highlighted that, despite finding some evidence for altered links between physiological signals and facial emotion perception in the two conditions, these results were highly specific. In most cases, the Bayesian analyses confirmed the null hypotheses, thus supporting the absence of group differences.

Conclusion

Altered integration of embodied emotional states has, to date, received little attention as potential mechanism of altered facial emotion perception in autism and social anxiety. Our study provides first insights in alterations in the link between physiological responses to facial emotion expressions and their perception. The results show that perceived emotional intensity of specific expressions was more strongly linked to physiological arousal in individuals with social anxiety compared to control participants, whereas it was less strongly linked to congruent facial muscle activations in individuals on the autism spectrum. Whether physiological resonance in terms of arousal has indeed a stronger weight in individuals with social anxiety and whether facial feedback is indeed less strongly integrated compared to neurotypical controls when interpreting emotionality in other's facial expressions should be examined further in future research.



Chapter 7

General discussion

Table 1. Brief overview of the methodology and key findings in each chapter

	Method	Key findings
2	Sample: N = 104, (1) zoo: n = 30; (2) festival: n = 22; (3) lab: n = 52 Task: Dot-probe task with faces (anger, happiness, fear, sadness, neutral) Self-reported traits: Social anxiety: M = 37.12 [4-83]; Autism: M = 18.27 [2-38] Measures: Reaction times	• Facial displays of anger, happiness, sadness and fear all elicited attentional biases • No robust evidence for a modulation of attentional biases by either social anxiety or autistic traits • Only in the Bayesian analysis, a decreased attentional bias towards happy expressions with higher autistic levels was found • Autistic trait levels and social anxiety trait levels showed a complex interplay in predicting attentional biases to anger expressions
3	Sample: N = 71, lab Tasks: (1) Passive viewing and, (2) Labelling of static facial and static bodily expressions (anger, happiness, fear, sadness, neutral), static emotional cues (tears, blush, dilated pupils) Measures: Facial muscle activity ("frowns"/"smiles"), skin conductance, cheek temperature, emotion recognition, confidence in recognition, perceived emotional intensity	• Both facial and bodily expressions of different emotions (anger, happiness, sadness and fear) were reliably recognized, with a pronounced advantage for happy faces (versus bodies) • No evidence for robust physiological response patterns in response to distinct emotional expressions, but robust… o facial mimicry of happy faces o early peak in skin conductance for angry faces o initial drop in cheek temperature for sad bodies • Facial expressions with tears strongly resonated in the observer, reflected by high perceived intensity ratings as well as a pronounced peak in skin conductance
4	Sample: N = 57, lab Tasks: (1) Passive viewing and, (2) Labelling of spontaneous, dynamic facial expressions (anger, happiness, fear, sadness, surprise, neutral) Measures: Facial muscle activity ("frowns"/"smiles"), emotion recognition, confidence in recognition, perceived emotional intensity Self-reported traits Social anxiety: M =38.53 [7-73]; Autism: M = 16.47 [2-39]	• Autistic and social anxiety traits showed distinct alterations in emotion perception o Higher autistic traits related to worse recognition of facial expressions o With higher autistic traits, mimicry was less predictive of emotion recognition o With higher social anxiety, confidence in emotion recognition was reduced, despite no actual differences in recognition performance

Table 1. continued

	Method	Key findings
5	Sample: (1) N = 99, online; (2) N = 100, lab Task: After viewing, direct labelling of spontaneous, dynamic facial expressions (anger, happiness, fear, sadness, neutral) + lab: heartbeat discrimination task Measures: Emotion recognition, confidence in recognition, perceived emotional intensity, trait interoceptive accuracy/sensibility + lab: facial muscle activity ("frowns"/"smiles"), cardiac interoceptive accuracy Self-reported traits: (1) Autism: M =17.05 [3-34]; (2) Autism: M = 17.30 [4-38]	• Recognition of anger (Experiment 1) and recognition of sadness (Experiment 2) were worse with higher autistic trait levels • Across both experiments, self-reported interoceptive accuracy did not explain worse recognition of specific emotional expressions with higher autistic levels • Self-reported interoceptive accuracy, objective (cardiac) interoceptive accuracy and facial mimicry were not systematically associated with emotion recognition accuracy • Yet, higher self-reported interoceptive accuracy, and less robustly also higher autistic trait levels, were linked to higher perceived emotional intensity of neutral expressions as well as more confidence in labelling them • While increases in facial muscle activations were more strongly linked to perceived emotional intensity with higher self-reported interoceptive accuracy, the opposite was observed for higher autistic trait levels
6	N = 107; clinical sample: Autism: n = 40; Social anxiety: n = 27; Control: n = 40 Tasks: (1) Passive viewing and, (2) Labelling of five spontaneous, dynamic facial expressions (anger, happiness, fear, sadness, neutral) Measures: Facial muscle activity ("frowns"/"smiles"), skin conductance, cheek temperature, emotion recognition, confidence in recognition, perceived emotional intensity, self-reported interoceptive accuracy/attention	Compared to controls… • Higher attention to bodily signals was shared in autism and social anxiety • Self-reported interoceptive accuracy was, in contrast, reduced in both conditions • Emotion recognition accuracy (anger, fear, sadness), perceived intensity of expressions (anger, fear happiness), confidence in emotion recognition (all including neutral) and mimicry of happy expressions were reduced in autism • While no robust evidence for altered facial emotion perception or altered physiological resonance was observed, with higher physiological arousal, sad facial expressions were perceived as more intense in social anxiety • Facial mimicry of anger was less strongly linked to perceiving higher emotional intensity in autism, which may be driven by lower self-reported interoceptive accuracy

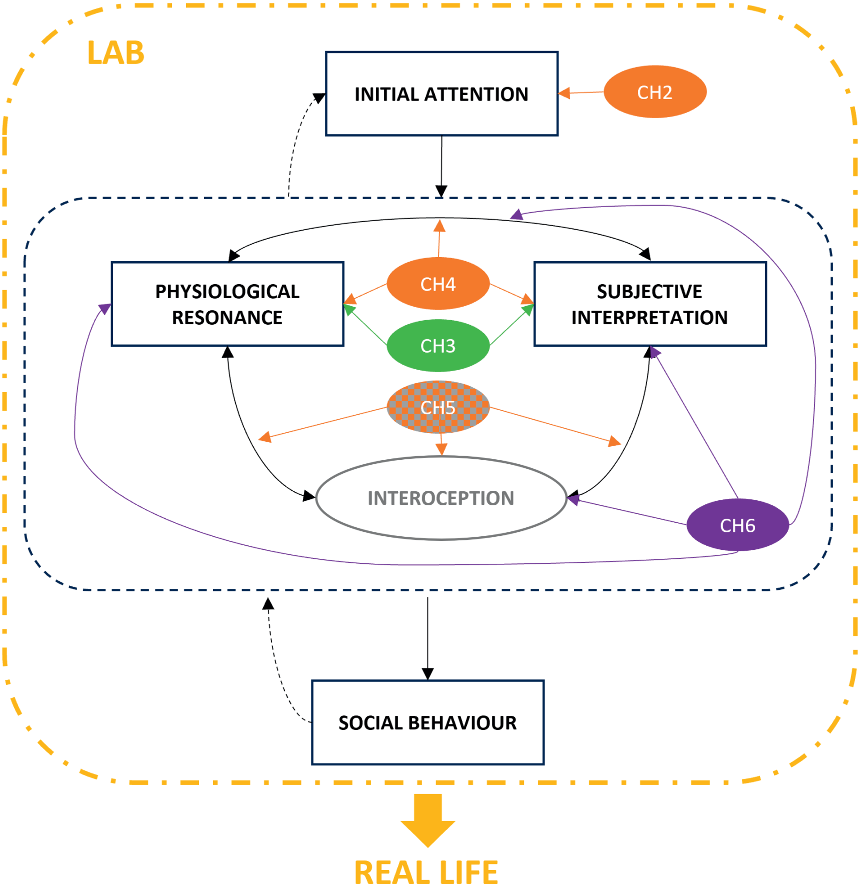


Figure 1. Illustration of the investigated (links between) processing stages and levels in identifying alterations in processing others' emotions in autism/social anxiety (trait levels) in each chapter. Colours represent the relevant characteristics of the examined sample (green = no individual differences, orange = social anxiety and autistic trait levels (checkered: autistic trait levels only), purple = diagnosis of autism or social anxiety). Chapter 2 examined differences in automatic responses towards emotional facial expressions associated with autistic and social anxiety trait levels at an early attentional stage. Chapter 3-6 all investigated effects of perceiving others' emotions on different levels (i.e., physiological resonance, subjective experience). Chapter 3 focused on the physiological resonance, represented in different bodily signals, and the interpretation of a diverse set of emotional expressions. Chapter 4 zoomed in on alterations in facial mimicry, confidence in emotion recognition and their links to facial emotion recognition associated with autistic and social anxiety trait levels. In addition to alterations in facial mimicry, Chapter 5 introduced individual differences in interoception as potential factor accounting for alterations in facial emotion perception associated with autistic trait levels. Building up on the findings of Chapter 3-5, Chapter 6 tested the hypothesized alterations in interoception and the (link between) physiological resonance (i.e., facial mimicry and emotional arousal) and subjective interpretation of facial expressions in individuals diagnosed with autism or social anxiety. Moving to real face-to-face interactions, an ongoing lab study explores individual differences in subjective experience, physiology and social behaviour (trust), as well as alterations in the link between physiological alignment between individuals and trust behaviour. As future goal, research should be conducted in more naturalistic settings, reflecting (alterations in) processing others' emotions in real life.

Theoretical Implications

While Table 1 provides a summary of the key findings by chapter, Figure 1 illustrates the overall framework, including all constructs of interest and their relations, and places the chapters in this framework. The remainder of this section discusses the integrated findings in the context of the literature. I will first provide separate summaries of findings related to facial emotion processing in autism and in social anxiety (trait levels), then contrast the resulting insights, and lastly also mention some general findings on facial emotion processing and the role of the body therein.

Alterations in Facial Emotion Processing Associated with Autism (Trait Levels)

The literature on (facial) emotion perception in autism predominantly suggests that emotions of others resonate less in individuals with autism. I examined indicators at various processing stages and levels, and I found, at least to some extent, support for this assumption. At an early attentional processing stage, which is generally characterized by biases towards emotional facial expressions in non-autistic individuals, a weaker bias related to autistic trait levels was found only, and not consistently, in the context of happiness displays (Chapter 2). Previous research with autistic samples mainly investigated biases towards anger displays and consistently described the existence of an attentional bias to social threat (i.e., angry faces) in autism (phrased as "intact", e.g., Fan et al. 2020). Considering the current findings in relation to autistic trait levels, it would be interesting to examine in how far this extends to other emotions, such as happiness, in individuals on the autism spectrum. My findings thus call for a broader investigation of modulations in attentional biases toward different emotions in autism.

The physiological resonance of emotions, as level of description within facial emotion processing, is commonly operationalized in terms of either facial mimicry or changes in physiological arousal. Although facial mimicry was not always affected in the same emotion categories across studies, the thesis overall shows weaker mimicry responses related to autism in non-autistic (apart from Chapter 3) and clinical samples. This general finding is in line with the vast literature on reduced facial mimicry in autism (Leung et al., 2023; Uljarevic & Hamilton, 2013). Potential alterations in physiological arousal in response to emotional expressions, indexed as changes in skin conductance, were only examined in Chapter 6, and no significant differences between individuals on the autism spectrum and controls were observed. In previous research, individuals on the autism spectrum showed reduced physiological arousal in response to others' emotion displays compared to controls specifically when the observed emotions had to be judged, and not only passively viewed (Hubert et al., 2009). Thus, not spontaneous, but rather, physiological arousal responses in the context of (instructed) facial emotion recognition might differ between individuals on the autism spectrum and non-autistic individuals. This could reflect different mechanisms used in the deliberate interpretation of emotional expressions. One could speculate that physiological responses in non-autistic individuals may be reinforced in an emotion recognition context but this requires further experimental investigation. Novel perspectives on altered facial emotion perception (Arnaud, 2020; Keating et al., 2023; Rutherford & McIntosh, 2007) indeed propose that different paths to emotion recognition, rather than simply "deficits", would explain worse performance in emotion recognition tasks in autism. Across my studies, I also found lower emotion recognition accuracies in both individuals on the autism spectrum and individuals with higher autistic trait levels. Accuracy for fearful expressions was particularly affected (Chapter 4 and Chapter 6), in line with some previous findings (Uljarevic & Hamilton, 2013). In my studies with non-clinical samples, perceived intensity of emotional expressions as well as confidence in their recognition was inconsistently reduced or increased for specific emotions as a function of autistic trait levels. The study with a clinical population (Chapter 6), however, showed a clear reduction in both being confident in the recognition of all facial expressions (including neutral) as well as in the level of perceived emotional intensity of most emotional expressions (angry, fearful, sad), in individuals on the autism spectrum compared to controls. This could be seen as another indicator of qualitative rather than quantitative differences in processing other's facial emotions in individuals on the autism spectrum compared to individuals with relatively higher autistic trait levels in the non-autistic population.

One component in which individuals might differ in processing others' emotions is the degree to which changes in one's own physiology, as a reflection of observed emotional states, are integrated in the subjective experience of others' emotions. I addressed this idea by linking the strength of facial muscle activity changes (Chapter 4-6), indexing facial mimicry, and of changes in skin conductance

(Chapter 6) indexing physiological arousal, to self-reports on facial emotion perception, and by investigating systematic modulations in those links associated with autistic trait levels (Chapter 4 and 5) or an autism diagnosis (Chapter 6). Findings suggest that non-autistic individuals with higher autistic trait levels and individuals on the autism spectrum might integrate changes in their facial muscle activity less in judging the emotional intensity of facial expressions, while there is only sporadic evidence for modulations in the link to emotion recognition accuracy. Importantly, observed effects were neither consistent across emotion categories within a study, nor across studies. The correlational design additionally only allows for interpretations based on plausibility rather than causality. Yet, these observations point out that differences in the sensation, integration and interpretation of internal signals might be a relevant factor in explaining altered (paths to) processing others' emotions in autism. Self-reported interoception indeed showed to be altered in individuals on the autism spectrum compared to controls but not depending on autistic trait levels in a non-clinical sample. Namely, individuals on the autism spectrum reported to be less accurate in judging their bodily signals while attending to them more strongly (Chapter 6). This is in line with the idea that various distinct bodily signals might be constantly overrepresented in autism but that access to signals of interest is difficult (Van de Cruys et al., 2017). As interoceptive signals are also assumed to influence the processing of others' emotions, differences in interoceptive abilities may partially explain altered facial emotion perception in autism. Simply speaking, as a result of less reliable information from the body, individuals on the autism spectrum may integrate cues from the body less strongly in the interpretation of emotional expressions. In my study with a clinical sample (Chapter 6), the less pronounced link between a bodily signal (corrugator activity) and the interpretation of an emotional expression (perceived intensity of anger) in autism was not significant anymore after including self-reported interoceptive accuracy, which showed a positive link to the perceived intensity of anger. While this is no direct evidence for the assumed role of interoception in altered facial emotion processing in autism, it still highlights that this perspective is an avenue worthwhile of future investigation. An increasing mechanistic understanding of interoception and its involvement in affective processing, including the bi-directionality of the link between subjective interpretations and bodily signals, builds the foundation for this avenue (Feldman et al., 2024).

Alterations in Facial Emotion Processing Associated with Social Anxiety (Trait Levels)

A heightened sensitivity to negative social-evaluative cues is central to cognitive-behavioral theoretical models on the development and maintenance of Social Anxiety Disorder (Heimberg et al., 2010; Hofmann, 2007; Rapee & Heimberg, 1997; Spence & Rapee, 2016). Evidence for this sensitivity has been previously established at early attentional stages in individuals with clinically diagnosed social anxiety, and also in individuals with heightened social anxiety but no diagnosis (Bantin et al., 2016b). Contrasting this literature, I did not find evidence that individuals with higher social anxiety trait levels would generally show an enhanced attentional bias towards angry faces (i.e., social threat; Chapter 2). Only when autistic trait levels were simultaneously low, higher social anxiety trait levels were associated with a stronger bias towards social threat. In those lines, some research indicates that, within a group of clinically relevant social anxiety trait levels, individuals differ in emotion-related attentional processes (Neophytou & Panayiotou, 2022). A more comprehensive picture of altered attention to emotions associated with social anxiety (traits) should therefore be obtained by considering additional individual characteristics that could explain variation within a sample of individuals with social anxiety, such as autistic trait levels.

Social anxiety was further not observed to be consistently related to differences in physiological responses to facial emotional expressions, both in a non-clinical and in a clinical sample. Similar to most previous research with inconclusive findings, these studies were conducted in laboratory settings. As physiological arousal, its perception and control over its expression seem to be altered specifically in real social contexts in social anxiety (Edelmann & Baker, 2002; Nikolić et al., 2015), most literature to date, including our studies, might not have been able to capture alterations in physiological responses to emotional expressions in real life. Chapter 6 indeed confirmed via self-reports that the sensation of physiological states in real life would differ between individuals with social anxiety and control participants. Individuals with social anxiety tend to attend to their bodily signals more while being less accurate in judging them. Higher interoceptive attention did, however, not play a role in the link between physiological arousal and perceived intensity of sad expressions, which was more strongly pronounced in individuals with social anxiety compared to controls (Chapter 6). Whether altered interoceptive processing might explain altered perception and potentially also altered integration of physiological arousal in processing social information remains to be seen.

Next to showing no evidence for an altered physiological resonance of emotional expressions, my studies in both clinical and non-clinical samples did not indicate that negative facial expressions would be recognized better or judged as more intense as function of social anxiety (trait levels). The presence, or at least anticipations of, a real social situation might be necessary to induce negatively biased processing of social information (Rapee & Heimberg, 1997). I nevertheless assumed that individuals with social anxiety and individuals with high social anxiety trait levels would show a reduced confidence in their emotion recognition skills, in line with their general beliefs about lower social skills (Voncken et al., 2020). Surprisingly, my expectations were only confirmed in the study with a non-clinical sample (CH4): individuals with higher social anxiety trait levels showed lower confidence in the recognition of all expression categories whereas there was only non-robust evidence for lower confidence in the recognition of sad expressions in individuals with clinically diagnosed social anxiety compared to controls. One potential explanation could be that one more emotion category, namely surprise, was included in the study with a non-clinical sample, rendering the task more difficult. Hence, it might be interesting to examine the extent to which social skill judgments in social anxiety are influenced by both task-related factors as well as the social nature of the context.

Distinct Alterations in Facial Emotion Processing in Autism and Social Anxiety (Trait Levels)

Despite their high comorbidity, this thesis provides evidence that a process linked to difficulties in social functioning, the perception of others' emotions, seems to be differentially affected in autism and social anxiety. Namely, I mainly observed evidence that the resonance of other's facial emotions, both on a physiological and on a experiential level, would be reduced in autism (or high autistic trait levels). Further, the link between the two levels also seems to be weaker, suggesting that physiological information (i.e., facial mimicry) might be less integrated in processing others' facial emotions. Thus, in line with the idea that individuals on the autism spectrum use different paths to recognizing others' emotions, they might follow this embodied path less than non-autistic individuals do.

Robust evidence for alterations in both the subjective experience of others' facial emotions and physiological responses linked to those expressions was not observed in social anxiety (or high social anxiety trait levels). I did, however, observe that physiological arousal was more predictive of the perceived intensity of sad expressions in individuals with social anxiety compared to controls. Sad expressions were also the only expression type for which individuals with social anxiety demonstrated lower confidence compared to controls in one experiment (Chapter 6). Hence, individuals with social anxiety might specifically rely on bodily signals to inform interpretations of other's expressions, if those are more difficult to identify. Importantly, expressions are often ambiguous in real situations (Aviezer et al., 2017) and individuals with social anxiety perceive physiological arousal, at the same time, more strongly (Edelmann & Baker, 2002). Following an embodied path to facial emotion perception in real-life settings could therefore also become maladaptive for individuals with social anxiety as they may judge others' emotions as more intense than actually displayed.

Contributions to the Facial Emotion Processing Literature

Next to expanding the knowledge on altered facial emotion perception in autism and social anxiety specifically, the current thesis also provides more fundamental insights into processing others' emotional expressions (in a non-clinical population). In line with their social-communicative function, the accumulated findings of this thesis underline the importance of non-verbal emotional expressions for human observers: They receive prioritized visual attention (Chapter 2) and are reliably recognized, when displayed via the face or the body (Chapter 3), and as static (Chapter 3) or dynamic facial stimuli (Chapter 4-6). Happy facial expressions seem to take a unique role within the distinct expression categories in that they are consistently recognized best (up to a ceiling performance) across studies (Chapter 3-6). As survival-relevant emotions are predominantly communicated via the face (App et al., 2011), the advantage in recognizing happy facial expressions (Kret, Stekelenburg, et al., 2013; Martinez et al., 2016) might reflect a motive that is highly relevant for survival in our modern society, namely affiliation. Accordingly, happy facial expressions are also most strongly, and almost exclusively, mimicked (Chapter 3 and Chapter 4), following the assumption that people would mainly mimic expressions promoting affiliation(A. Fischer & Hess, 2017). Whether mimicry of happy facial expressions would help their recognition, via sensorimotor simulation (Wood et al., 2016), could unfortunately not be evaluated within this thesis, given that there was too little variation in happiness recognition performance. Yet, some evidence for the sensorimotor simulation account comes from findings linking stronger corrugator activity ("frowning") to higher accuracies in the recognition of negative expressions (Chapter 4 and Chapter 6, however not Chapter 5). The conditions under which sensorimotor (facial) simulations play a role in facial emotion recognition require future investigations. It should further be acknowledged that happy expressions were the only emotional expression of positive valence in our studies. Additionally, they are the most frequently encountered facial emotional expression in daily life (Calvo et al., 2014). High recognition accuracy could consequently also result from their distinctiveness within the task context as well as their high familiarity.

While basic-emotion specific changes in autonomic nervous system activity are only sporadically described in Chapter 3 of the current thesis, this chapter highlights that physiological changes might specifically be evoked in response to more subtle and uncontrolled emotional cues, such as tears. Being genuine indicators of physiological arousal in the expressor (Kret, 2015) that are more difficult to control than muscle activity underlying emotional facial expressions, their resonance should also become particularly apparent in autonomic nervous system measures of the observer and might relate to their perception. Hence, future research should investigate the role of facial cues (e.g., dilated pupils, tears or a blush) more strongly in the context of the perception of basic emotions, but also of more complex emotions, such as blushing in the context of embarrassment or pride (Nikolić et al., 2016, 2019; Riddell et al., 2023).

As broadly outlined in the introduction, I believe interoception to be one relevant factor in explaining to which extent changes in one's own physiology link to interpretations of observed emotional expressions. The examination of this idea is, however, challenging, provided the complex nature of the multi-dimensional (e.g., accuracy vs. awareness) and multimodal (e.g., cardiovascular vs. respiratory) construct of interoception (Suksasilp & Garfinkel, 2022). Contrasting findings on shared variance between subjective and objective measures of interoceptive accuracy (Murphy et al., 2020), I did not observe that people who perceive themselves as more accurate in sensing their bodily signals (i.e., trait interoceptive accuracy) would actually be more accurate in judging whether their heartbeat is in sync with a series of tones or not (i.e., objective interoceptive accuracy; Chapter

5). Furthermore, against my expectation, neither subjectively-reported nor objectively-measured interoception predicted how well emotional expressions are recognized. Yet, self-reported interoceptive accuracy did play a role when it came to the link between actual physiological changes linked to viewing expressions and their perceived emotional intensity (Chapter 5 and Chapter 6). Namely, people with higher trait interoceptive accuracy seem to integrate the strength of changes in their facial muscle activity more in perceived emotion expression intensity ratings, even if the muscle activity does not reflect mimicry patterns (Chapter 5). Whether this reflects a higher sensitivity to muscle changes (low-level) or a stronger integration of interoceptive signals in cognitive processing (higher level) is one of the many questions which will keep interoception researchers busy in the future.

Methodological Considerations

The studies in this thesis encompass different populations (students, general public, individuals with clinical diagnoses), different experimental settings (online, public spaces, laboratory), different emotion-processing tasks (dot-probe, passive viewing of facial emotional expressions, facial emotion recognition), different stimuli (static and acted facial/bodily expressions, static and manipulated facial emotion cues, dynamic and spontaneous facial expressions) and different analysis methods (e.g., Frequentist versus Bayesian analyses). As a result of applying a wide variety of methods and comparing findings across studies, this thesis provides relevant methodological insights in studying (alterations in) facial emotion perception.

First and foremost, I initially conducted studies in non-clinical and mainly student samples, before testing my hypotheses in a study with a clinical sample. This is common practice in clinical research, in order to identify relevant processes, formulate hypotheses and adjust paradigms if necessary (e.g., Pollmann et al., 2010). By only involving clinical populations after careful pilot studies, the burden for these participants, who are vulnerable and difficult to recruit, is aimed to be reduced. Nevertheless, especially when formulating hypotheses based on non-clinical pilot studies, researchers automatically follow the assumption that clinical samples mainly differ from non-clinical samples with varying clinical trait levels in the extent to which an outcome is affected. The proposition of a "continuum of impairment", with clinical conditions lying at the extreme of trait levels in the general population, has been made with regard to both social anxiety (Rapee & Spence, 2004) and autism (Robinson et al., 2011). Also in a diagnostic context, a dimensional approach to assessing mental health conditions, instead of sole classification, has been put forward in the DSM-V (American Psychiatric Association, 2013). Interestingly, in all my non-clinical studies, a substantial number of participants reported on social anxiety trait level scores of clinical relevance, according to empirically-derived cut-off scores (Mennin et al., 2002; Rytwinski et al., 2009). Clinically-relevant autistic trait levels, in contrast, were only reported in singular cases and very close to the predefined cut-off score (Baron-Cohen et al., 2001). This observation matches the higher prevalence of social anxiety in the general population. Furthermore, it highlights that autism, as a neurodevelopmental condition, is associated with qualitative differences in cognitive processing, which might not necessarily occur to a lesser degree in neurotypical individuals (Sasson & Bottema-Beutel, 2022). In my studies, both non-autistic individuals with higher autistic trait levels and individuals on the autism spectrum showed reduced emotion recognition, as well as, in some cases, reduced facial mimicry and a reduced link between mimicry and facial emotion perception. Yet, confidence in emotion recognition and perceived emotional intensity of expressions were mainly reduced in the clinical sample, as was self-reported interoceptive accuracy. In how far this might be a reflection of qualitative different processing styles, or paths to emotion recognition, or quantitative differences in similar processing styles is still an open question.

When conducting studies with non-clinical samples, researchers often constrain themselves to testing members of the student population. These individuals are typically young, highly-educated, and, in the case of Psychology students, female. Gender-, age- or socioeconomic status-effects thus likely bias the results. Moreover, experimental studies are usually conducted in laboratory settings. Those allow for a high control of environmental influences but extract the individual from a familiar setting and its stimulations/distractions. In two of my studies, I addressed this issue by testing a more diverse sample in public spaces (Chapter 2) and online (Chapter 5), in addition to laboratory sessions with students. In Chapter 2, I did not observe any meaningful influence of testing in public spaces, compared to a laboratory setting, on experimental outcomes (i.e., attentional biases). By making the participation in experiments more accessible to the general public, researchers can accomplish two things at once: they can involve taxpayers more strongly in research, following a citizen science approach, as well as have more generalizable results without necessarily obscuring their effects of interest. Especially during the COVID-19 pandemic, research transitioned from physical laboratories to online platforms. With the development of better tools to perform research online, researchers often continued to choose online over in-person setting, reaching a large and diverse audience in little time. When comparing findings from the exact same task in an online versus laboratory setting in Chapter 5 (with the exception of facial muscle activity sensors in the lab), many, yet not all, findings could be replicated. Thus, as it is generally recommended in psychological research, studies should be replicated, and it seems particularly interesting to see which effects hold when the setting changes. While, from a functional perspective, emotional signals should be processed and interpreted similar across settings, contextual influences in processing others' emotions, such as observing a smile in a funeral versus a wedding context (Kastendieck et al., 2021), have been described in the literature, and should therefore not be neglected.

The different studies within this thesis not only employed different tasks to target different stages in facial emotion processing, but also experimented with different task parameters. One example of this is the nature of the (facial) emotional expressions. In the first two experimental chapters of this thesis, commonly-used static images of acted expressions from the NimStim database were used (Tottenham et al., 2009). Results in studies on facial emotion perception in autism (Enticott et al., 2014; Keating & Cook, 2020; Rigby et al., 2018), and sporadically also in social anxiety (Torro-Alves et al., 2016), show specific alterations in processing dynamic compared to static facial expressions. Moreover, acted stimuli are exaggerated representations of prototypical facial expressions and do not represent the subtlety with which emotional expression can appear in daily life. For these reasons, our research group developed a new stimulus set of spontaneously evoked, dynamic emotional expression with a controlled background and matched timing, based on the FEEDTUM database (Wallhoff et al., 2006). The development of this stimulus set then allowed us to test facial emotion perception of more naturalistic stimuli than used in most previous work, while the standardization procedure still allowed us to compare our results to those studies. Although my studies remained consistent in the usage of stimuli after their development, different variations of the facial emotion recognition task were created by changing the task demands.

In two chapters of this thesis (Chapter 4 and Chapter 5), I investigated modulations in facial mimicry and in its link to facial emotion perception by autistic trait levels in a non-clinical student population. In Chapter 4, facial mimicry was significantly associated with facial emotion recognition, and this link was modulated by autistic trait levels for sad expressions. In Chapter 5, in contrast, there was no evidence for such a link, let alone for a modulation by autistic trait levels. Findings linking facial mimicry to emotion recognition are known to be inconsistent (Holland et al., 2020), and our observations could provide a potential explanation: In Chapter 5, task demands (i.e., labeling the expressions among others) were already known to the participants during the viewing of the expressions, with the ratings directly appearing after each expression. Chapter 4, on the contrary, consisted of a separate passive viewing phase (during which facial muscle activations were measured) and a subsequent labelling phase (during which the expressions were rated). When not being primed with task demands, leaving more ambiguity, people might show more spontaneous mimicry (i.e., without having potential responses pre-activated), which could be integrated in later qualitative judgments of expressions. When all potential categories and the task to judge expressions according to those are already known during viewing, people might rather match activated mental representation to the presented stimuli (Keating & Cook, 2023). While qualitative interpretations might be less influenced by bodily feedback in this scenario, it might still reinforce quantitative judgments about the intensity of an observed emotional experience or the confidence in making the qualitative judgment. This might specifically be the case for people with higher (self-reported) interoceptive accuracy, as described in the Chapters 5 and 6. Although these assumptions still need to be tested, researchers should be aware that apparently small changes in experimental paradigms might have the potential to activate different processing modes.

Lastly, in an attempt to model the data of each study best, I employed a variety of analysis methods. In my studies, effects of interest were mainly rather small and presented themselves in complex three-way-interactions. Multi-level modeling allowed me to include multiple observations of each participant, while accounting for their dependency. Importantly, the interpretation of coefficients in these models are highly dependent on the model definition, such as whether one level of a variable serves as reference (treatment coding) or whether the coefficient of each level relates to the average effect of all levels (sum coding). To answer specific questions, such as whether there is a significant relation to the outcome in a specific group, additional post-hoc comparisons (e.g., slope comparisons against zero for continuous variables) are necessary. Thus, researchers should be careful in interpreting their model fits, and be aware whether they are actually able to answer their questions, based on the model definition. Moreover, the robustness of observed (small) effects is often questionable and the ideal of normally distributed outcome data, or at least residuals, often does not match reality. Under the guidance of my colleague Tom Roth, I employed Bayesian statistics to address these issues. Namely, in the majority of my studies, I defined Bayesian multi-level models in addition to Frequentist multi-level models, thereby gaining more insight in the robustness of results. Furthermore, in Chapter 6, in which the sample size of the social anxiety group was low, Bayesian statistics allowed me to evaluate whether there was enough evidence for the alternative hypothesis, and also for the null hypothesis. The Bayesian approach further allowed me to model data distributions that were difficult to capture in commonly-used model families in Frequentist analyses. Rating scales, for example, are not always interpreted as continuous, with most people choosing middle values. In my studies, I observed that people sometimes tend to choose extremes over middle values in their confidence ratings (Chapter 5) or that they interpret scales in a more ordinal than continuous way, with distances not being equal between all data points (Chapter 6). Bayesian modeling allowed me to translate these observations in models, using generalized linear mixed models with a zero-one-inflated family (Chapter 5) and sequential mixed models with an s-ratio family (Chapter 6). Exploring the nature of collected data and searching for well-suited approaches to analyze them is a necessary step for researchers to obtain confidence in their results.

Practical Implications

Before directly evaluating the results of this thesis in the light of clinical practice, I would like to discuss an important implication which is related to my personal motivation to conduct psychological research. Progressing through my Bachelor's and Master's education, I became more and more aware of how different people's experiences in our shared world can be, given their past experiences but also their predispositions. By nature, people have different ways to process their environment and this environment, in turn, influences how they will perceive future environments. Our actions are strongly intertwined with our perceptions, which can explain why others sometimes seem to act "weird" to us: they just differ in their way of processing what is happening in the world, including their own selves, and have a different action repertoire linked to that. In our society, mental disorders as well as neurodevelopmental conditions, are a framework to classify differences that have a significant impact on the life of an individual or the people around them. Within the present thesis, I am looking at an everyday process in which people differ and which has consequences for coordinating our social world, namely making sense of other people's emotions. Here, I specifically examine systematic differences in their processing at different stages, including different levels of description, related to autism and social anxiety. Learning about these differences allows us to (1) acknowledge diversity in processing social information and understand unexpected responses and (2) identify under which circumstances specific processing styles might be more beneficial than others and how those could be promoted. Hence, instead of judging the "typicality" of others' behaviors and trying to tune them to behaving "typical", our interactions can benefit from being more sensitive to others' differences and mutually attuning to reach a better understanding.

That being said, there might be situations in which different ways of processing social information, as observed in autism and social anxiety, contribute to difficulties in navigating the social world. For example, while matching perceived emotional expressions to visual mental representations might work well for clear exemplars, many expressions in daily life are highly variable, mixed and ambiguous (Aviezer et al., 2017). Here, rather than comparing those to existing visual mental representations, it may be more beneficial to include different information in their interpretation, such as from embodied simulations. Although causality as well as the exact mechanisms still need to be established, my research indicates that this type of information is less integrated in processing others' emotions in autism (and high autistic trait levels). A less accurate sensation of relevant bodily signals, or their prioritization (Van de Cruys et al., 2017) might be one relevant factor here, as indicated by the reduced self-reported interoceptive accuracy in my research as well as reduced objective interoceptive accuracy in previous work (Garfinkel et al., 2016; Z. J. Williams et al., 2023). Preliminary evidence for the effectiveness of interoceptive training (Aligning Dimensions of Interoceptive Experience, ADIE), specifically targeting the dimension of accurately sensing bodily signals, has already been described in a randomized controlled trial with individuals on the autism spectrum (Quadt et al., 2021). Outcomes specifically related to being aware of one's emotions did not significantly change between the ADIE training group and the active control group, but seemed to improve for both groups. This might be explained by the type of training which the active control group received, namely recognizing and matching emotional prosody. Next to a reduced interoceptive accuracy, individuals on the autism spectrum also report an increased attention to bodily signals (Chapter 6) and difficulties in integrating and interpreting them (Fiene et al., 2018). Interventions that focus on mindfulness or the appraisal of bodily signals might be a promising avenue to improve interoceptive abilities at these specific interoceptive dimensions (Heim et al., 2023). Hence, training interoceptive abilities at different dimension directly within, or at least linking to, an emotion recognition context could facilitate a more embodied path to emotion recognition in autism.

Across studies, we only find little alterations in facial emotion processing associated with higher social anxiety trait levels or clinically diagnosed social anxiety compared to controls. Although the absence of evidence does not translate into evidence of absence, it seems unlikely that profound differences within the studies have not been identified. Hence, within laboratory settings, individuals with social anxiety (or high trait levels) might not differ in the way they process emotional expressions. Bodily responses to others' expressions as well as their integration in judging their emotionality might also be relatively similar, apart from a stronger integration of physiological arousal when judgments are more difficult. Importantly, especially in social anxiety, processing other's emotions in a real social context differs from processing them in a lab context (Dijk, Fischer, et al., 2018). In real contexts, cognitive biases are assumed to be activated that, among others, lead to a vigilance to social-evaluative cues (emotional expressions) and an increased perception of physiological arousal (Heimberg et al., 2014). Here, findings a higher sensitivity to negative facial expressions compared to controls is highly likely. Moreover, an embodied path to emotion recognition might become maladaptive, as too much self-related physiological arousal could be misattributed to the perception of the other. Compared to the lab experiments in this thesis, individuals with social anxiety (or high trait levels) further show a more robust underconfidence in their social performance in studies in real-life scenarios (Dijk et al., 2009; Kashdan & Savostyanova, 2011; Voncken & Bögels, 2008). This decreased confidence is thought to develop in negatively biased post-event processing of social situations (Dannahy & Stopa, 2007; Helbig-Lang et al., 2016), and might be specific to the situational context. General interventions focusing on overcoming cognitive biases, like Metacognitive Training (MCT; see Nordahl & Wells, 2018), might therefore also be effective in targeting difficulties in social functioning, including altered perception of others' emotional expression in real social situations. Additionally, interventions focusing on an accurate perception of interoceptive signals or on a regulation of attention to interoceptive signals in a social context could prevent the disproportionate perception and potential misattribution of physiological arousal in social anxiety.

Limitations and Future Directions

Studying social cognition with computerized paradigms in the lab differs immensely from the dynamic processes occurring in real-life social interactions. Instead of purely observing social stimuli, information flow in interactions is bi-directional, with the interaction partners being aware of each other and influencing each other's cognition and behaviour. When knowing that others can see us, we act more according to social norms and, for example, stare at others (Laidlaw et al., 2011), and specifically their eyes (Gobel et al., 2015), less. On the flipside, we also behave more socially towards real others, by showing clearer facial expressions (Frith, 2009) and by acting more prosocial (Cañigueral & Hamilton, 2019). To capture these intrinsic features of real social interactions, the call for a second-person approach in research on social cognition and behaviour has been made less than a decade ago (Schilbach, 2015b).

In line with this development, the initial goal of my PhD project was to start investigating facial emotion processing in a more controlled setting from the perspective of a passive observer (third person), and to move to more dynamic, naturalistic situations as a next step. Due to unforeseen delays and challenges within my PhD trajectory, including long waiting times in the communication with the medial ethics committee and the Covid-19 pandemic, I eventually conducted most of my studies in a laboratory setting using computerized, non-interactive tasks. As a consequence, the current thesis is limited in the degree to which it can capture alterations in facial emotion processing in real life. For example, individuals with higher social anxiety trait levels seem to avoid staring at another person that is physically present more compared to individuals with lower social anxiety traits (Howell et al., 2016; Konovalova et al., 2021). In contrast, the effect of being watched by others is suggested to be less pronounced in individuals on the autism spectrum, as a result of less self-referential processing elicited by less mentalizing (Cañigueral & Hamilton, 2019). Differential attention to others in real-life situations might thus contribute to alterations in the processing of their (facial) emotional expressions. Furthermore, responses to others seem to be differentially modulated by the presence of a real social context in social anxiety versus autism: While individuals with social anxiety control their (emotional) expressions more strongly in social situations, including when mimicking others' facial expressions (Dijk, Fischer, et al., 2018), individuals on the autism spectrum seem to adjust their behavior less according to social norms compared to controls (Izuma et al., 2011). Cognitive biases elicited by a real social context are thought to create an even stronger effect on behaviour in social anxiety, whereas audience effects in autism seem to be weaker. Across the chapters of this thesis, I only observed limited evidence for alterations in facial emotion processing associated with social anxiety (trait levels). Whether alterations in social anxiety or high social anxiety trait levels become more apparent in real social settings, and whether the presence of others influences facial emotion processing less in autism, compared to controls, should be investigated in future studies.

Going beyond effects of other individuals' physical presence, studies employing face-to-face interaction paradigms allow to capture bi-directional dynamics in the perception and responding to spontaneous expressions of interaction partners. Decreased spontaneous coordination of behaviours (often referred to as "interpersonal synchrony") has been identified in interactions between individuals on the autism spectrum and controls (Georgescu et al., 2019; Peper et al., 2016), and even considered a diagnostic marker of autism (Koehler et al., 2022). In contrast, coordination in movements between individuals with social anxiety and controls has specifically been found to be less synchronous when it was intentional, and not spontaneous (Varlet et al., 2014). Non-verbal behaviours associated with heightened stress levels in interactions, such as fidgeting, seem to form an exception here. If those behaviours are spontaneously shown by individuals with social anxiety, controls as interaction partners have a strong tendency to adopt them. This observation resulted in the claim that negative behaviours and experiences, as expression of social anxiety, would be contagious in interactions with individuals with social anxiety (Heerey & Kring, 2007; Park et al., 2010; Shaw et al., 2021), whereas the reciprocity of positive affect would be reduced (see also Pearlstein et al., 2019). Next to observable behaviours, past research has specifically highlighted alignment in autonomic nervous system measures (i.e., physiological synchrony) as indicator of affiliation (attraction; Prochazkova et al., 2021) as well as prosocial behaviour (i.e., cooperation; Behrens et al., 2020) in social interactions. Despite the known alterations in non-verbal signal processing in autism and social anxiety, only few studies with clinical samples have looked at alterations in physiological synchrony in interactions. In parent-child interactions, in which physiological synchrony is most commonly researched in autism, physiological synchrony seems to be lower if the child has an autism diagnosis, compared to controls, and if the symptomology is more severe (Baker et al., 2015; H. Wang et al., 2021). Modulations in physiological synchrony between an individual with social anxiety and a control, compared to two controls, seem to depend on the content of a conversation: while closeness-generating conversations typically elicit higher physiological synchrony in controls, synchrony is reduced with higher social anxiety levels in dyads with a member with social anxiety (Asher et al., 2020, 2021). Yet, little is known about the role of altered automatic alignment in physiology and its direct relations to social behaviour in interactions between individuals on the autism spectrum or individuals with social anxiety and controls.

To address this gap in the literature, I developed a non-verbal, interactive trust game paradigm together with my colleague Fabiola Diana and the engineer Elio Sjak-Shie, in which the visibility of the previously unknown interaction partner could be manipulated. The employment of various measures, such as eye-tracking, video recordings, self-reports, heart rate and skin conductance, allows us to track the exchange of visible signals, associated physiological changes and subjective experiences, as well as their link to behaviour in a trust context. While data collection with the clinical subsamples is still ongoing, preliminary analyses of the role of autistic traits and social anxiety traits in the control group offer interesting preliminary insights (Folz et al., 2024). Looking at the self-reported experience, the higher social anxiety traits were, the more individuals perceived themselves as less confident and, additionally, overestimated negative perceptions by their partners (i.e., being seen as less confident). This mirrors previous work on negatively biased self-related beliefs in social situations in high social anxiety traits (Kashdan & Savostyanova, 2011) as well as in social anxiety (Hirsch & Clark, 2004). Partners, in contrast, were rated as more attractive and, surprisingly, more similar to oneself with higher social anxiety traits. Autistic traits were exclusively linked to ratings of the interaction itself, which was experienced as more awkward by individuals with higher autistic traits. When linking subjective experience to trust behaviour, trustworthiness ratings of the partner were less associated with monetary investments in individuals with higher social anxiety traits when the partner was visible (versus not). Hence, in face-to-face interactions with others, individuals with higher social anxiety trait levels may base their trust behaviour on different information than the perceived trustworthiness of their partner. Looking at a different level of description, I did not observe robust evidence for alterations in physiological synchrony associated with either autistic traits or social anxiety traits. Yet, with higher social anxiety traits, heart rate synchrony was less positively associated with monetary returns to partners, independent of whether they were visible or not. Prosocial behaviour may, thus, have been less motivated by being "in tune" with others in individuals with high social anxiety trait levels. Future analyses including the clinical subgroups will help to understand to which degree (altered) subjective experiences and (altered) physiological alignment may play a role in (alterations in) a fundamental building block of social relations, namely to trust others.

Importantly, when conducting real-life social interaction research, not only characteristics of the person of interest but also of their interaction partner should be taken into account. Generally, we tend to surround ourselves with people who are similar to us (Bolis et al., 2021). Clinical research, however, mainly pairs dissimilar interactants, one individual with a condition and a control without a condition, to investigate social functioning. Hence, observed difficulties might reflect differences in processing styles between individuals, rather than "deficits" of one individual, as proposed by the dialectical misattunement hypothesis (Bolis et al., 2018) or the "Double Empathy problem" (Milton, 2012). Individuals with stronger differences in processing and experiencing the environment are assumed to align less easily with each other, compared to more similar individuals, including two individuals with the same condition (e.g., autism). In support of this assumption, some studies have shown that individuals on the autism spectrum tend to have more positive experiences in interactions with other individuals on the autism spectrum compared to interactions with non-autistic individuals (Crompton et al., 2020; Morrison et al., 2020). Moreover, they tend to be more accurate in judging facial expressions posed by individuals on the autism spectrum (Lampi et al., 2023). Yet, other researchers highlight alterations specific to autism in biological and behavioural rhythmicity, including in establishing synchrony with others (Baldwin et al., 2022; Bowsher-Murray et al., 2022; Tordjman et al., 2015). Eventually, altered interpersonal synchrony may arise from a combination of characteristics of the individual and the dyad in autism (McNaughton & Redcay, 2020).

Research on the role of misattunement in social interaction difficulties in social anxiety is scarce. If social anxiety traits are low in an interaction partner, individuals with high social anxiety traits expect to be perceived more negatively (Kashdan & Savostyanova, 2011), experience less closeness in interactions (Kashdan & Wenzel, 2005) and in the formation of friendships (Boucher et al., 2015). In how far a mismatch in social anxiety traits (or in diagnoses) affects the processing of others' expressions and immediate feelings of connectedness is, to date, still unknown. In my preliminary analysis of the interactive trust game data, I also included differences in autistic traits and social anxiety traits between the partners in a dyad in predicting subjective experiences, physiological synchrony, and their link to trust behaviour. When the difference in social anxiety traits was higher in a dyad, partners were evaluated as less trustworthy and as less close to the self. Additionally, when the partner was visible, the feeling of closeness was more strongly linked to monetary investments in dyads with a smaller difference in social anxiety scores. Thus, interactions between more attuned individuals in terms of social anxiety traits may indeed result in more positive experiences, impacting interaction outcomes. I did not observe any effects related to autistic trait level differences, which might be owing to the limited range of autistic traits in the non-clinical sample. Supporting the spotlight on qualitatively different processes and experiences in neurodivergent populations, misattunement might only become relevant in interactions between different neurotypes, such as a neurotypical individual and an individual on the autism spectrum (Sasson & Bottema-Beutel, 2022).

While I have already discussed constraints linked to testing non-clinical samples earlier, it is additionally important to mention that individuals diagnosed with the same condition are not a coherent group. The “spectrum” in “Autism Spectrum Conditions” highlights this variability, as does the identification of different social anxiety subtypes (D’Avanzato & Dalrymple, 2016). When it comes to facial emotion processing, only few studies have examined variability in autism. Here, observations of a worse emotion recognition performance have indeed only been driven by a subgroup within a sample of individuals on the autism spectrum (Meyer-Lindenberg et al., 2022), with those individuals also showing most social difficulties in real life (Loth et al., 2018). One personality trait that has specifically received attention in altered emotion processing in autism, but also other conditions, is alexithymia. Alexithymia is defined as an inability in expressing, describing, or distinguishing among one’s emotions (first introduced by Nemiah et al., 1976) and is highly prevalent in autism (49.93%, Kinnaird et al., 2019). Even though the prevalence of alexithymia itself has not been as systematically investigated yet, individuals with social anxiety report difficulties in identifying and describing their emotions. The origin of reports of co-occurring alexithymia in both autism and social anxiety has recently been suggested to lie in altered interoceptive processing (Murphy et al., 2017; Palser et al., 2018). A vast amount of research support a prominent role of alexithymia in both emotion processing and interoception in autism (e.g., Bird & Cook, 2013; Ketelaars et al., 2016; D. Trevisan et al., 2019; D. A. Trevisan et al., 2016). Some studies have even concluded that mainly alexithymia, and not autism symptomology per se, would account for alterations in interoception (Shah et al., 2016), emotion recognition performance (Cook et al., 2013) or subjective and objective emotional arousal after emotion induction (Gaigg et al., 2018). In Chapter 6, I observed that both individuals on the autism spectrum and individuals with social anxiety report higher alexithymia. Although controlling for alexithymia did not change the results of my analysis, I believe that alexithymia may play an important role in processing emotions of others’ in autism and social anxiety, especially in the integration of a bodily resonance of others’ emotions.

Lastly, research on physiological synchrony in clinical practice highlights both the relevance and the potential of considering interpersonal affective dynamics in the clinical context (Coutinho et al., 2014). Namely, therapists and patients who are more strongly linked on a physiological level do not only have more positive interactions on the short term but also better therapeutic outcomes (Kleinbub, 2017; Marci & Orr, 2006). Interventions employing music, rhythmic movement and dance can foster a dynamic, affective engagement with others, as in everyday life social interaction, by inducing or facilitating synchrony among individuals (Manders et al., 2022; Veid et al., 2023). Yet, factors determining the success of these interventions need to be further studied (Marquez-Garcia et al., 2022).

Conclusion

Difficulties in daily social interactions have a severe negative impact on the quality of life in individuals on the autism spectrum and in individuals with social anxiety. The goal of the current dissertation was to zoom in on one aspect that contributes to successful communication, namely the processing of others' non-verbal emotional expressions. In order to obtain a comprehensive and integrative picture of potential shared and distinct alterations, I investigated how the perception, the resonance and the interpretation of other individuals' (facial) emotional expressions, including links between different levels of description, are modulated by varying trait levels associated with autism and social anxiety as well as in the respective clinical diagnoses. Next to replicating findings of a decreased resonance of facial emotional expressions in higher autistic trait levels and autism with regard to both physiology (i.e., facial mimicry) and interpretation (i.e., emotion recognition and perceived emotional intensity), my studies emphasize potential alterations in the links between the two levels. Namely, individuals on the autism spectrum (or with higher autistic trait levels) may integrate physiological information less in interpreting others' emotional expressions. Differences in interoceptive processing in autism may play a role here, likely reinforcing a less embodied path to processing others' emotions. Using typical lab-based facial emotion processing paradigms, I did not observe strong and consistent evidence for specific alterations associated with social anxiety (trait levels). Some of my studies, including ongoing work, suggest that negatively-biased self-beliefs might influence the processing of and responding to emotional expressions, particularly in real-life interactions with others. Namely, individuals with social anxiety may expect to be judged more negatively by their interaction partners, influencing the interpretation of their expressions as well as the confidence in evaluating them. Furthermore, a stronger integration of bodily arousal, due to heightened attention to bodily signals, might result in interpreting others' expressions as more emotionally charged. When combined with a negatively biased perception of others' expressions, an embodied path to interpreting others' emotions may become maladaptive in social anxiety. Taken together, I believe that an investigation of the resonance of others' emotional expressions and its link to their interpretation is a promising approach to a better understanding of social interaction difficulties in both autism and social anxiety, despite the divergence in the specifics of alterations in the two conditions. Minding the body in research on cognitive processing has already proven its necessity in various fields, from low-level visual processing to high-level meta-cognitive processes. Given the intrinsically embodied nature of emotions as well as humans being social creatures, studying the physiological resonance of others' emotions from a functional perspective promises a better understanding of how we navigate our social world.

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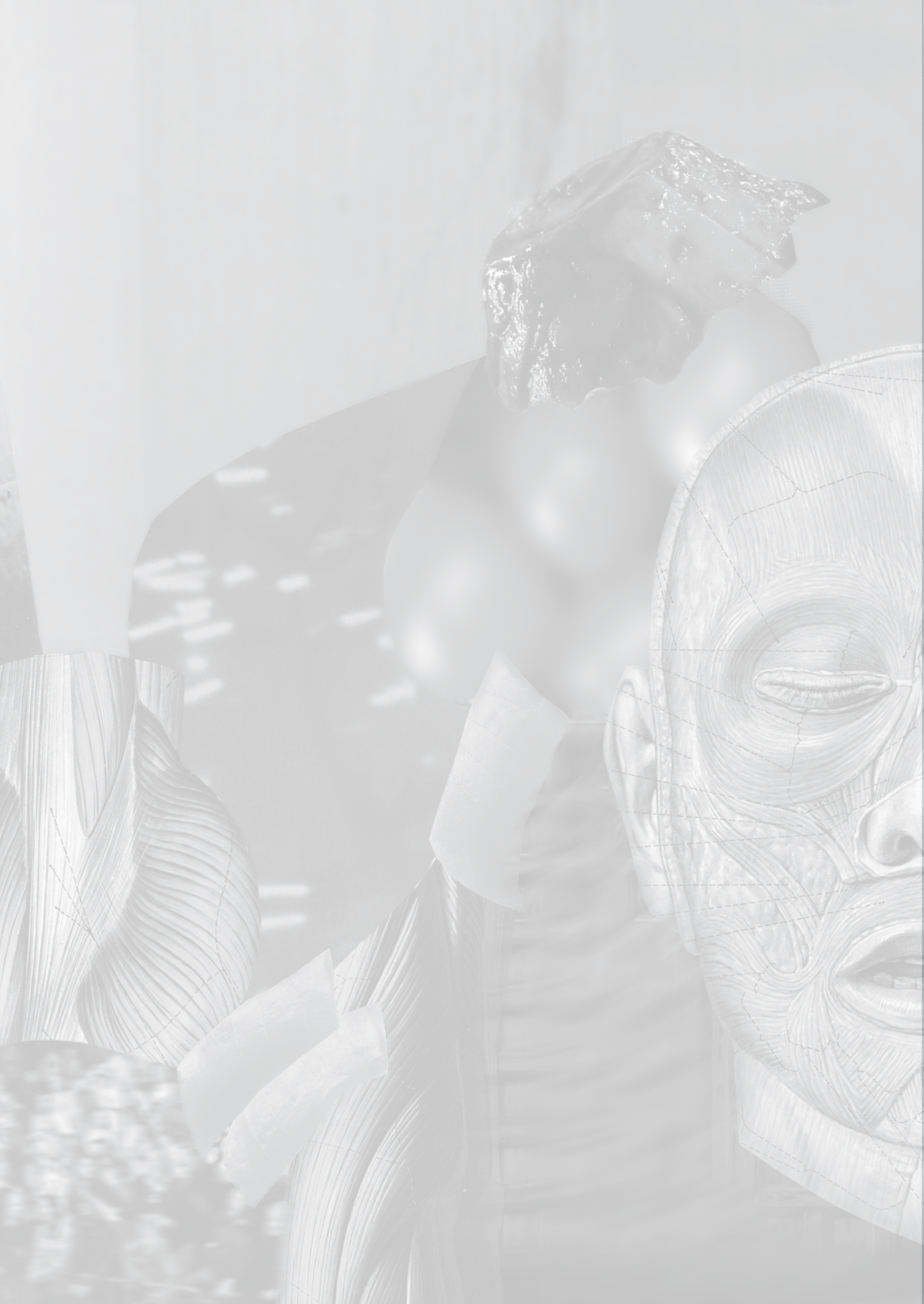

Samenvatting

Resonerende emoties: Een embodied perspectief op veranderingen in de verwerking van gezichtsemoties bij autisme en sociale angst

Begrijpen wat anderen voelen en wat hen bezighoudt, vormt de basis voor succesvolle sociale relaties, van eenmalige ontmoetingen met vreemden tot levenslange vriendschappen en relaties met familie of romantische partners. Kennis over anderen wordt doorgaans verworven in directe interactie met hen. Hoewel dit voor veel mensen automatisch gaat, kunnen mensen op het autismespectrum en mensen met sociale angst moeilijkheden ondervinden bij het navigeren van zulke sociale interacties. Als gevolg daarvan ondervinden ze vaak uitdagingen bij het succesvol aangaan van sociale relaties. Omdat mensen sociale dieren zijn en onze sociale omgeving cruciaal is voor ons welzijn, is het belangrijk om te begrijpen welke kenmerken van sociale interacties de navigatie ervan bemoeilijken. Een kenmerk van dagelijkse interacties dat het begrijpen van anderen bijzonder moeilijk maakt, is dat gedachten en gevoelens niet altijd worden uitgesproken. Mensen uiten informatie soms non-verbaal, bijvoorbeeld via gezichts- en lichaamsuitdrukkingen, kleine gebaren of geluiden. Het uiten van dit soort informatie kan opzettelijk gebeuren, zoals het tonen van een grote glimlach om de waardering voor een cadeau aan te geven. Vaak kunnen uitdrukkingen echter ook onbedoeld ontglippen en iemands ware gevoelens onthullen. Stel je een situatie voor waarin je de uitnodiging van je beste vriend voor zijn bruiloft afwijst en hij met betraande ogen zegt: 'Het is oké'. Het herkennen van zijn verdriet in het gezicht, ondanks zijn accepterende woorden, kan ertoe leiden dat je je keuze heroverweegt en een belangrijke vriendschap redt. De manier waarop dit verdriet, en emotionele gezichtsuitdrukkingen in het algemeen, worden herkend, kan per persoon en situatie verschillen. In dit voorbeeld ben je misschien al gealarmeerd, omdat je weet hoe belangrijk het voor je vriend is om al zijn dierbaren bij belangrijke gelegenheden bij elkaar te hebben. Daarom zou je systematisch kunnen controleren op tekenen van verdriet in zijn gezicht, zoals hangende mondhoeken of betraande ogen. Een andere bron van informatie is de automatische spiegeling van de emotionele uitingen van anderen. Net als muziek kunnen geuite emoties van anderen in ons lichaam resoneren. Bovendien kunnen ze in ons lichaam worden gesimuleerd, aangezien onze lichamen veel op elkaar lijken en we in het verleden waarschijnlijk soortgelijke emotionele ervaringen hebben gehad. Terugkomend op ons voorbeeld: het zien van de betraande ogen kan er ook voor zorgen dat de tranen ook bijna in jouw ogen springen, wat aangeeft dat er iets mis is.

Interessant is dat mensen op het autismespectrum en mensen met sociale angst, naast moeilijkheden bij de interpretatie van emotionele uitdrukkingen, ook de neiging hebben om verschillen te vertonen in de automatische reacties op de gezichtsemoties van anderen. Dit is vooral het geval wanneer de verdrietige uitdrukking van een vreemde is en niet van een vriend. In dit geval zou je op basis van eerder onderzoek kunnen verwachten dat iemand op het autismespectrum de verdrietige uitdrukking minder spiegelt en deze ook als minder verdrietig ervaart. Een persoon met sociale angst kan daarentegen meer van streek raken, wat tot uiting komt in een sterke lichaamsreactie, en kan de uitdrukking als negatiever ervaren. In hoeverre verschillen in lichamelijke reacties verband houden met verschillen in de interpretatie van emoties van anderen bij autisme en sociale angst, is echter nog niet voldoende onderzocht. Dit onderwerp is bijzonder relevant omdat zowel mensen op het autismespectrum als mensen met sociale angst informatie uit hun lichaam anders lijken te verwerken dan de algemene bevolking. Het niet nauwkeurig kunnen detecteren van veranderingen in het lichaam, of het niet goed kunnen evalueren van deze veranderingen in de huidige context, kan het gebruik van lichamelijke informatie bij het begrijpen van de emoties van iemand anders verder bemoeilijken. Binnen dit proefschrift was het mijn doel om de kennis uit te breiden over hoe automatische lichamelijke reacties op emotionele gezichtsuitdrukkingen van anderen verband houden met interpretatie van de uitdrukkingen, en hoe deze processen variëren bij mensen op het autismespectrum of met sociale angst. Ik heb dit doel door middel van meerdere stappen benaderd, die terugkomen in verschillende hoofdstukken van mijn proefschrift. Het is belangrijk om te benadrukken dat in de eerste hoofdstukken van mijn proefschrift mensen zonder de diagnose autisme of sociale angst deelnamen aan mijn onderzoek. In plaats daarvan vroeg ik mijn deelnemers om in vragenlijsten persoonlijke kenmerken te rapporteren die verband houden met autisme en sociale angst. Dit is een gebruikelijke benadering in psychologisch onderzoek. Het biedt namelijk een eerste glimp van wat je kan verwachten als je mensen met een klinische diagnose zou betrekken, zonder ze zelf te testen. Daardoor krijgen kwetsbare mensen minder verzoeken om deel te nemen aan mogelijk uitputtende onderzoeken. Bovendien voorkomt het dat de onderzoeker moeilijke wervingsprocedures moet doorlopen. In het laatste hoofdstuk van dit proefschrift (en in lopend onderzoek) breid ik deze eerste inkijk uit naar mensen met een klinische diagnose van autisme of sociale angst.

Nadat ik in hoofdstuk 1 een algemene inleiding op het onderzoeksonderwerp heb gegeven, begin ik in hoofdstuk 2 met het onderzoeken van de allereerste reacties op de gezichtsuitdrukkingen van anderen. Mijn experiment vond plaats op drie verschillende locaties, waardoor ik verschillende mensen in verschillende settings kon testen: dierentuinbezoekers, bezoekers van een wetenschapsfestival en studenten. Op alle drie de locaties heb ik gekeken hoe mensen met verschillende niveaus van autisme- en sociale angstkenmerken aandacht besteden aan verschillende gezichtsuitdrukkingen van emoties. De methode die ik gebruikte om hun aandacht voor emoties te meten, wordt de 'dot-probe taak' genoemd. Deelnemers moeten op een stip tikken die willekeurig achter een van twee afbeeldingen van gezichtsuitdrukkingen verschijnt die tegelijkertijd kort naast elkaar worden weergegeven. Hoewel de persoon op beide afbeeldingen dezelfde is, toont de ene afbeelding een emotionele uitdrukking (bijvoorbeeld blijdschap) terwijl de ander een neutrale uitdrukking laat zien. Als deelnemers sneller reageren op de stip wanneer deze achter de emotionele uitdrukking verschijnt vergeleken met wanneer de stip achter de afbeelding met een neutrale uitdrukking verschijnt, heeft de emotionele uitdrukking waarschijnlijk van tevoren de aandacht getrokken. De aandacht kan bijvoorbeeld automatisch worden getrokken door een lachend gezicht en daar blijven hangen omdat het misschien leuk is om met deze persoon te communiceren. Eerdere onderzoeken hebben zich vooral gericht op één specifiek type emotie om dit fenomeen te onderzoeken, ook wel 'aandachtsbias' genoemd. In onderzoek naar autisme en sociale angst was deze emotie vooral woede. Als iemand boos naar je kijkt, is het van groot belang dat je daar onmiddellijk aandacht aan besteedt, aangezien je mogelijk gevaar loopt. Mensen met sociale angst zijn doorgaans nog alerter op woede-uitingen dan mensen zonder diagnose, omdat ze bang zijn voor negatieve reacties van anderen. Hoewel mensen op het autismespectrum over het algemeen minder beïnvloed worden door de emotionele uitingen van anderen, is hun aandacht volgens eerdere onderzoeken nog steeds sterk gericht op woede-uitingen in vergelijking met neutrale uitingen. Deelnemers aan mijn onderzoek vertoonden een vergelijkbare aandachtsbias voor uitdrukkingen van woede, blijdschap, verdriet en angst. Dit was een nieuwe bevinding binnen de literatuur, die zich tot dan toe vooral op één emotie had geconcentreerd. In tegenstelling tot eerdere onderzoeken waarin een sterkere aandachtsbias werd gevonden naar uitingen van woede bij mensen met een hoge mate van sociale angstkenmerken, vertoonden deelnemers met hogere sociale angstkenmerken in mijn onderzoek over het algemeen geen sterkere aandachtsbias voor woede. Ze vertoonden alleen een sterkere bias voor woede-uitingen als hun niveaus van autistische kenmerken tegelijkertijd laag waren. Alles bij elkaar genomen kunnen we concluderen dat emotionele uitingen over het algemeen de aandacht trekken. Om kleine verschillen tussen individuen te begrijpen moeten onderzoekers rekening houden met meerdere kenmerken van een individu.

Als volgende stap onderzocht ik in hoofdstuk 3 hoe mensen lichamelijk reageren op de emotionele uitingen van anderen en hoe zij deze uitingen interpreteren. Tot nu toe is er niet veel onderzoek gedaan naar verschillende soorten emotionele uitingen, verschillende lichamelijke reacties daarop en verschillende manieren van interpretatie. Ik heb daarom besloten dit onderzoek uit te voeren zonder rekening te houden met klinische kenmerken of diagnoses, en me in plaats daarvan te concentreren op een uitgebreidere beschrijving. Ik liet mensen indicatoren van emoties in het gezicht zien (tranen, blozen en verwijde pupillen) en volledige emotionele uitingen (woede, blijdschap, verdriet en angst) die via het gezicht of het lichaam tot uiting kwamen. Voor de lichamelijke reacties heb ik de spiegeling van gezichtsuitdrukkingen, zweten en blozen gemeten. In dit hoofdstuk en in al mijn volgende hoofdstukken zijn verschillende aspecten van het interpreteren van emoties beoordeeld door de deelnemers te vragen de emotie een label te geven, het vertrouwen in hun oordelen te beoordelen, en te beoordelen hoe intens de emotie leek. Mensen waren over het algemeen goed in het herkennen van emoties in het gezicht en het lichaam. Vooral blije gezichten werden heel gemakkelijk herkend, terwijl dit bij blije lichamen minder het geval was. Lichamelijke reacties waren echter niet zo gemakkelijk te onderscheiden bij de deelnemers voor verschillende emotionele uitingen. Echter, bij het kijken naar gezichtsspieren die de gezichtsuitdrukkingen weerspiegelen, konden duidelijke verschillen tussen emoties, en vooral de spiegeling van blije gezichtsuitdrukkingen, worden waargenomen. Bovendien vertoonden mensen een toename van zweten bij het bekijken van betraande en boze gezichten, terwijl er minder gebloosd werd bij het bekijken van verdrietige lichamen. Al met al stellen onze lichamelijke reacties ons misschien niet direct in staat emoties van anderen af te leiden. Ze zouden echter hun interpretatie kunnen vergemakkelijken, bijvoorbeeld wanneer we een blije uitdrukking spiegelen. Bovendien kunnen lichaamsreacties zoals zweetreacties ons voorbereiden om actie te ondernemen in belangrijke situaties. Ze kunnen bijvoorbeeld de weg banen voor een ruzie met een boze persoon of voor het troosten van een in nood verkerend persoon. Hoewel deze activering zeer relevant lijkt bij het bepalen van hoe we ons tegenover een andere persoon gedragen, lijkt het ons niets te vertellen over de specifieke emoties die de ander ervaart.

In Hoofdstuk 3 en eerder onderzoek bleek het spiegelen van gezichtsuitdrukkingen, of zogenaamde gezichtsmimicry, het meest te variëren tussen verschillende gezichtsuitdrukkingen. Daarom leek het ook de meest geschikte vorm van lichamelijke feedback om de gezichtsemoties van anderen te helpen interpreteren. Voortbouwend op deze inzichten heb ik mij in hoofdstuk 4 geconcentreerd op de verschillen die samenhangen met autistische en sociale angstkenmerken bij gezichtsmimicry, en ook op de relatie ervan met het interpreteren van emotionele gezichtsuitdrukkingen. Daarnaast wilde ik weten of mensen die minder vertrouwen hadden in het herkennen van uitdrukkingen er ook daadwerkelijk slechter in waren. Mensen met sociale angst worden onzeker over hun vaardigheden in sociale situaties en zien zichzelf vaak negatiever. Dit kan er ook toe leiden dat ze hun vermogen om emoties te herkennen onderschatten. Mensen op het autismespectrum zijn daarentegen misschien niet zo goed in het evalueren van hun vaardigheden in sociale situaties. Of deze verschillen in zogenaamde metacognitieve oordelen - dat wil zeggen, het vermogen om na te denken over en te evalueren hoe men zelf en anderen functioneren in sociale situaties - bijdragen aan moeilijkheden bij het interpreteren van de emoties van anderen, is nog niet onderzocht. Daarom heb ik twee mogelijke bronnen van feedback overwogen: gezichtsmimicry en metacognitieve oordelen. Bovendien liet ik, in tegenstelling tot de meeste eerdere onderzoeken waarin geacteerde gezichtsuitdrukkingen werden gebruikt, video's zien van gezichtsuitdrukkingen die spontaan waren opgenomen. Deze uitdrukkingen, die ik ook in alle volgende hoofdstukken gebruikte, zijn veel beter vergelijkbaar met het echte leven, omdat de opgenomen persoon echte emoties kon uitdrukken zonder instructies of de opname in gedachten te hebben. De spontane uitingen (woede, blijdschap, angst, verdriet, verrassing en neutraal) werden over het algemeen ook goed herkend door de studenten die aan mijn onderzoek deelnamen. Mensen met hogere versus lagere autistische kenmerken hadden echter lagere herkenningspercentages.

Interessant is dat hun gezichtsmimicry minder sterk verband hield met het nauwkeurig herkennen van sommige uitdrukkingen. Bij hogere autistische kenmerken en mogelijk ook bij autisme lijkt lichamelijke feedback dus minder bij te dragen aan het begrijpen van de emoties van anderen. Deze verschillen werden niet waargenomen met betrekking tot sociale angstkenmerken. Wanneer mensen hogere (versus lagere) sociale angstkenmerken hadden, onderschatten ze echter hoe goed ze uitdrukkingen in alle emoties herkenden. Dit kan te wijten zijn aan algemene negatieve overtuigingen die mensen met sociale angst kunnen hebben over hun sociale vaardigheden, waardoor hun oordeel op dat moment wordt beïnvloed. Deze negatief vooringenomen oordelen kunnen vervolgens negatieve overtuigingen versterken, waarbij deze vicieuze cirkel het in stand houden van sociale angst bevordert.

In mijn volgende hoofdstuk wilde ik inzoomen op een vermogen dat, zelfs intuïtief, relevant lijkt bij de integratie van lichamelijke feedback bij het begrijpen van andermans emoties. Ik onderzocht of interoceptie – het vermogen om interne lichamelijke signalen waar te nemen – een rol speelt bij verschillen in de interpretatie van de emotionele gezichtsuitdrukking van anderen. Ik heb me in hoofdstuk 5 gericht op de verschillen gerelateerd aan de niveaus van autistische kenmerken om twee redenen: Ten eerste leek gezichtsmimicry een zwakkere link te tonen met de manier waarop gezichtsemoties worden geïnterpreteerd door mensen met hogere niveaus van autistische kenmerken in hoofdstuk 4. Moeilijkheden bij interoceptie zijn ook vaak gedocumenteerd in de algemene autismeliteratuur. Er was dus een brede theoretische basis voor het onderzoek naar de rol van interoceptie bij de herkenning van gezichtsemoties. Ten tweede heb ik voor dit onderzoek gegevens verzameld op twee verschillende tijdstippen tijdens de Covid-19-pandemie. Die tijden werden tot op zekere hoogte overschaduwd door beperkingen en de angst voor besmetting. Omdat onze vragenlijst voor sociale angst gedeeltelijk de motivatie meet om mee te doen en je op je gemak te voelen bij sociale activiteiten, zijn zulke vragenlijsten tijdens de pandemie mogelijk geen goede weerspiegeling van de daadwerkelijke sociale angst. Als gevolg van een lockdown tijdens de pandemie vond het eerste experiment van dit hoofdstuk online plaats. Hierdoor konden we alleen zelfrapportages beoordelen over hoe nauwkeurig iemand hun interne signalen kan waarnemen, en kon ik gezichtsmimicry op de gepresenteerde uitdrukkingen niet beoordelen. Om een completer beeld te krijgen, voerde ik later een onderzoek uit in het laboratorium, waarbij ik gezichtsmimicry en interoceptiemetingen kon verkrijgen. Hoewel ik opnieuw opmerkte dat mensen met hogere versus lagere niveaus van autistische kenmerken sommige gezichtsuitdrukkingen minder nauwkeurig herkenden, speelden noch interoceptie, noch gezichtsmimicry hier een rol. Deze tegenstrijdigheid met hoofdstuk 4 en mijn aanvankelijke verwachting kan worden verklaard door verschillen in de manier waarop deelnemers de taak benaderden. Ze wisten van tevoren al dat ze emoties zouden moeten herkennen, en hebben misschien specifiek naar hints gezocht bij het bekijken van de uitdrukkingen. Echter waren bij mensen met hogere versus lagere niveaus van autistische kenmerken veranderingen in de eigen expressie minder sterk geassocieerd met hoe intens zij de bekeken expressie waarnamen. Hoewel er sprake is van een ander aspect dan in hoofdstuk 5, kan lichamelijke feedback dus minder geïntegreerd zijn in de interpretatie van de uitdrukkingen van anderen bij mensen met hogere niveaus van autistische kenmerken. Ook het idee dat interoceptie in deze context relevant kan zijn, werd gesteund. Mensen met een hogere versus lagere zelfgerapporteerde nauwkeurigheid bij het waarnemen van interne signalen rapporteerden namelijk een hogere intensiteit van de bekeken uitdrukkingen wanneer er grotere veranderingen in hun eigen uitdrukkingen waren. Het beter kunnen waarnemen van interne signalen kan de integratie van lichamelijke feedback bij het begrijpen van de emoties van anderen vergemakkelijken.

In de laatste studie die in Hoofdstuk 6 in dit proefschrift is opgenomen, heb ik mijn onderzoek uiteindelijk uitgebreid naar mensen op het autismespectrum en mensen met een diagnose van sociale angst. Op deze manier kon ik testen of de verschillen die ik tot dan toe had waargenomen op vergelijkbare wijze tot uiting komen bij mensen bij wie de diagnose werd gesteld vanwege moeilijkheden in het dagelijks leven. Daarom volgde ik een vergelijkbare aanpak als in mijn eerdere onderzoeken voor het meten van lichamelijke reacties (gezichtsmimicry en zweetreacties) en de interpretatie (herkenning, vertrouwen in herkenning en waargenomen intensiteit) van spontane, op video opgenomen gezichtsuitdrukkingen (woede, blijdschap, angst, verdriet en neutraal). Uit zelfrapportage over interoceptie bleek dat, vergeleken met mensen zonder enige klinische diagnose (controlegroep), zowel mensen op het autismespectrum als mensen met sociale angst sterker op interne signalen letten. Tegelijkertijd meldden ze allebei dat ze minder nauwkeurig zijn in het waarnemen van deze signalen. In lijn met mijn eerdere bevindingen en de bredere literatuur waren mensen in het autismespectrum ook minder nauwkeurig in het beoordelen van sommige emotionele uitingen vergeleken met de controlegroep. Bovendien bootsten ze blije uitdrukkingen minder na, hadden ze minder vertrouwen in het labelen van alle uitdrukkingen en ervoeren ze sommige uitdrukkingen als minder intens vergeleken met de controlegroep. Toen ik inzoomde op het verband tussen lichamelijke reacties en interpretatie, vond ik ook enige steun voor de verschillen tussen mensen op het autismespectrum en mensen uit de controlegroep. Een sterkere weerspiegeling van woede-uitingen hield namelijk minder sterk verband met de perceptie ervan als intenser bij mensen in het autismespectrum, vergeleken met controlepersonen. Net als bij mensen met hogere niveaus van autistische kenmerken, is lichamelijke feedback mogelijk niet zo sterk geïntegreerd in de interpretatie van emotionele uitingen bij autisme. Dit kan opnieuw worden veroorzaakt door moeilijkheden bij de interoceptie. Mensen met sociale angst waren daarentegen zeer vergelijkbaar met controlepersonen in hun reactie op en interpretatie van emotionele gezichtsuitdrukkingen. Ze verschilden alleen van de controlegroep in termen van een sterker verband tussen de zweetreactie bij het zien van verdrietige uitdrukkingen en de waargenomen intensiteit van die uitdrukkingen. Omdat verdrietige uitdrukkingen nogal moeilijk te identificeren zijn, kunnen mensen met sociale angst onzekerder zijn en sterker afhankelijk zijn van lichamelijke feedback wanneer ze met zulke uitdrukkingen geconfronteerd worden. Dit soort suggesties zijn een waardevolle inspiratiebron voor toekomstig onderzoek.

In mijn laatste hoofdstuk, hoofdstuk 7, reflecteer ik op de observaties en inzichten die mijn PhD-traject hebben opgeleverd. Ik ben van mening dat mijn gecombineerde bevindingen benadrukken dat lichamelijke reacties en hun integratie in het begrijpen van de emoties van anderen niet mogen worden verwaarloosd bij het onderzoeken van sociale interactiemoeilijkheden bij autisme. Ze wijzen verder op interoceptie als een proces dat zou kunnen helpen begrijpen hoe en waar de integratie verzwakt zou kunnen worden. Hier moet rekening worden gehouden met verschillen in subprocessen, bijvoorbeeld de nauwkeurige sensatie van één bepaalde lichaamsreactie versus de integratie van meerdere reacties. Bovendien zijn observaties mogelijk niet voldoende. We moeten ook op een gecontroleerde manier reacties genereren (d.w.z. vergelijkbaar voor alle mensen) en meten hoe deze worden gevoeld en hoe deze zich verhouden tot het interpreteren van de emoties van anderen om daadwerkelijk verschillen in interoceptie als oorzaak te kunnen identificeren. Belangrijk is dat een verminderde integratie van lichamelijke feedback bij het begrijpen van de emoties van anderen niet noodzakelijkerwijs slecht is. Er zijn andere manieren waarop emoties correct kunnen worden herkend, bijvoorbeeld door het gezicht van iemand anders te scannen op duidelijke indicatoren, zoals getrokken liphoeken. Als deze echter niet duidelijk zichtbaar zijn, kan een flexibele aanpassing aan andere manieren, zoals lichamelijke feedback, helpen. Mensen op het autismespectrum kunnen daarom baat hebben bij interventies gericht op lichaamsbewustzijn en, meer specifiek, interoceptie. Mijn conclusies met betrekking tot sociale angst zijn sterk verankerd in de bestaande literatuur over het ontstaan en het in stand houden van de aandoening. Het is bekend dat mensen met sociale angst veelal ongerechtvaardigde negatieve opvattingen hebben over hun sociale vaardigheden en veel stress in hun lichaam ervaren in sociale situaties. Wanneer ze proberen emoties bij anderen te identificeren, verwachten ze mogelijk negatieve reacties van anderen en is hun interpretatie van uitingen mogelijk al negatief gekleurd. Het ervaren van het lichaam als meer geactiveerd kan er bovendien toe leiden dat er ten onrechte wordt aangenomen dat de als negatief waargenomen uitingen van de ander intenser zouden zijn. Omdat ik binnen de reikwijdte van dit proefschrift geen observaties heb gedaan in echte sociale situaties, is dit slechts een aanname die in toekomstig onderzoek moet worden getest. Het trainen van lichaamsbewustzijn en interoceptieve vaardigheden kan ook nuttig zijn voor mensen met sociale angst in bredere zin. Het kan hen helpen een nauwkeuriger beeld te krijgen van hun lichaamsactivatie en, als onderdeel van interoceptie, leren hoe ze stress in sociale situaties kunnen reguleren.

Samen biedt mijn proefschrift een nieuw perspectief op de rol van de belichaming van de emoties van anderen – door het waarnemen en integreren van lichamelijke reacties – bij moeilijkheden bij het begrijpen van de gezichtsemoties van anderen bij autisme en sociale angst.

Curriculum vitae

Julia Folz was born in Ulm (Germany) on December 23, 1993. Already during her time as student at the Robert-Bosch-Gymnasium in Langenau, she developed a strong interest in understanding the drivers of human behaviour. After her graduation in 2012, she therefore started a Bachelor's degree in Psychology at Heidelberg University. During her time as a Bachelor student, Julia got engaged in research as a student assistant in various departments of the Psychological Institute, including Social Psychology, Developmental and Biological Psychology, and a research group on self-regulation. She also explored research possibilities outside of academia, by joining the SINUS Markt-and Sozialforschung GmbH for a six-months internship. Her inspiring research internship stays at the Affective Brain lab at University College London and the Biological Psychology Department at the University of Tübingen eventually convinced her to continue her journey in academia. These internship experiences additionally fostered Julia's interest in studying physiological processes in the context of emotion. As a result, she decided to investigate the neurophysiological emotional response to aesthetic stimuli in her Bachelor thesis under supervision of Prof. dr. Hagemann, which she completed in 2016. In order to extend her knowledge and skills concerning experimental research, Julia joined a Master's degree in Neuro-cognitive Psychology at LMU Munich, for which she received a scholarship by the Max Weber Program, in the same year. Throughout her Master studies, Julia continued to work as a student assistant in the EEG & Behavior Lab at LMU. Her fascination with the description of dynamics in social interactions eventually led her to join the Research Group "Social Neuroscience" at the Max-Planck-Institute of Psychiatry for her Master thesis in 2018. Under the supervision of Prof. dr. med. Leonhard Schilbach and dr. Dimitris Bolis, Julia investigated the role of alignment between real-time interacting individuals in decision-making on multiple levels, namely subjective experience, gaze and neural activity. In 2019, Julia joined the Comparative Psychology and Affective Neuroscience (CoPAN) lab at Leiden University to obtain a PhD in Cognitive Psychology under supervision of Prof. dr. Mariska Kret and dr. Milica Nikolić. Building up on her interests and experiences, her PhD project focused on physiological processes in the non-verbal communication of emotions. As potential mechanism of social interaction difficulties, she particularly zoomed in on alterations associated with autism and social anxiety in the embodiment of others' emotions and in its linkage to emotion perception. Julia's project involved a collaboration with Prof. dr. med. Katja Kölkebeck at the LVR hospital in Essen. There, PhD student Kristina Nikić conducted experiments with clinical samples, i.e., individuals on the autism spectrum and individuals with social anxiety, which were planned and overseen by Julia. A Leiden University Fund (LUF) travel grant enabled Julia to establish another collaboration by joining Prof dr. Winkielman's Social Cognition lab at UCSD (San Diego) for a summer research stay in 2022. During her time abroad, she could apply her interest in embodied emotions to a new field, namely politics. In the scope of her PhD research, Julia engaged in various teaching activities. In addition to the supervision of Bachelor and Master thesis projects as well as internships, Julia gave lectures in courses, workgroups and in workshops on topics such as experimental methods, social cognition in psychopathology and emotion research. Following her passion to discuss research with peers, Julia not only attended various conferences and summer schools but also resumed organizing events, which she already engaged in during her Bachelor and Master studies (e.g., the Heidelberger symposium in 2014 and various TedxTUM events). Together with her PhD colleague Chris Riddell, Julia organized a symposium on (embodied) emotions and social connectedness across disciplines at the conference of the European Society for Cognitive Psychology in 2023. Moreover, Chris and Julia applied for funding to organize a mini-conference on positive and negative consequences of interpersonal alignment, the "Co-Align 2023", which was awarded a LUF conference grant. Next to sharing her findings with other scientists, Julia wrote several popular science blogs for the Leiden Psychology Blog to make her PhD research accessible to the general public. In 2024, Julia started a position as Postdoc in the Developmental Psychopathology group at the University of Amsterdam. Here, she is studying how mothers attune to their infants to help them regulate their emotions, and how this relates to the infants' ability to regulate themselves.

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