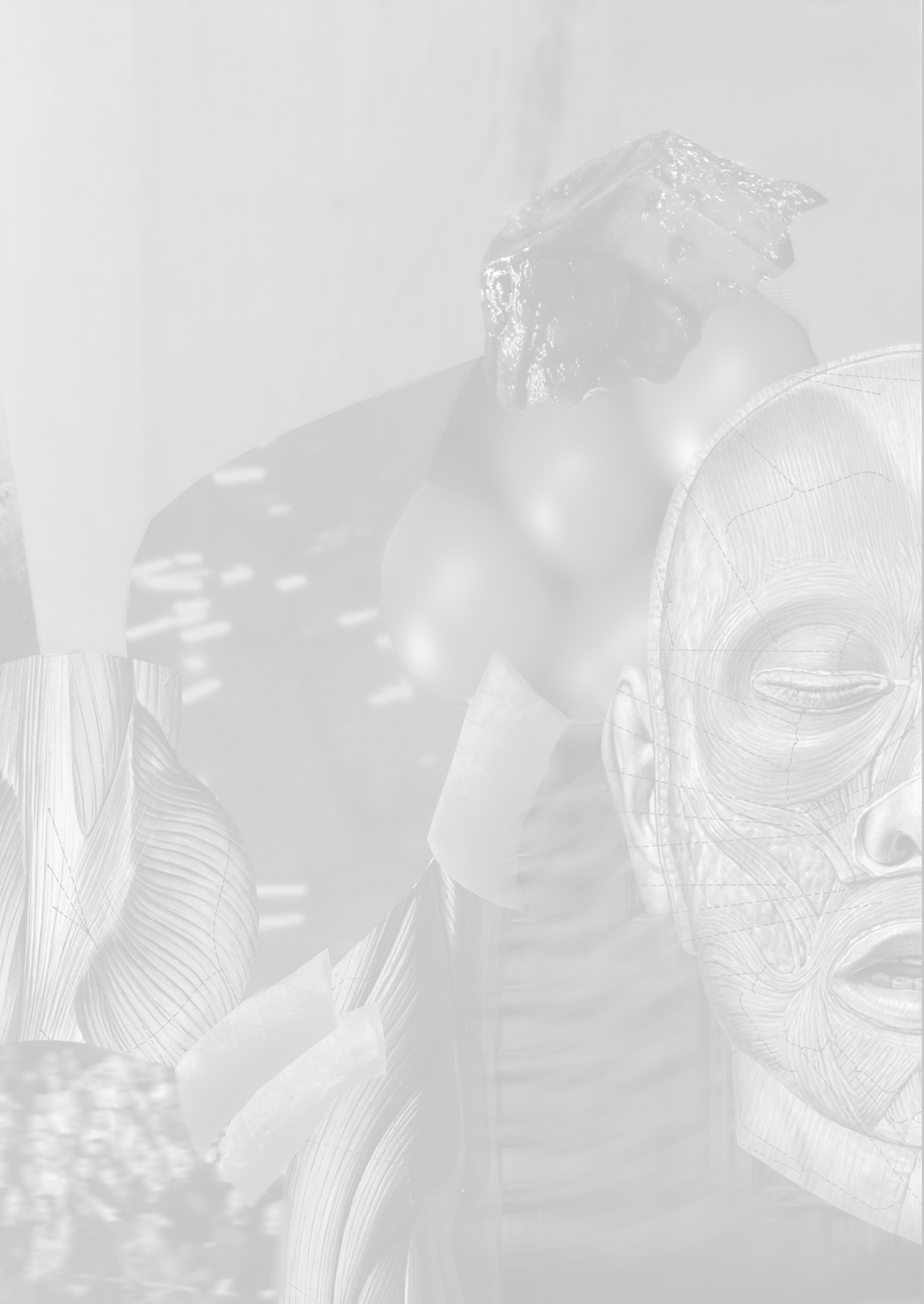
Resonating emotions: an embodied perspective on alterations in facial emotion processing in autism and social anxiety

Folz, J.



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

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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

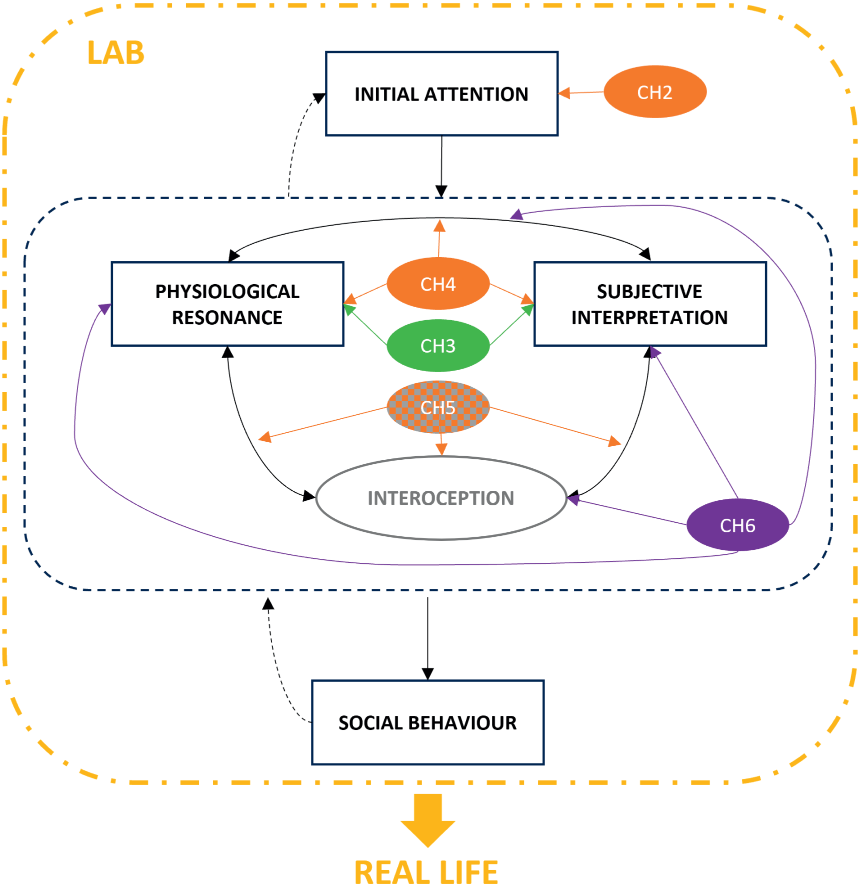

Figure 1. Illustration of the investigated (links between) processing stages and levels in identifying alterations in processing others' emotions in autism/social anxiety (trait levels) in each chapter. Colours represent the relevant characteristics of the examined sample (green = no individual differences, 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.